Limnological Conditions in Ice-Covered Lakes, Especially as Related to Winter-Kill of Fish

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Contribution from the Michigan Institute for Fisheries Research

A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the University of Michigan.

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LIMNOLOGICAL CONDITIONS IN ICE-COVERED LAKES, ESPECIALLY AS RELATED TO WINTER-KILL OF FISH

INTRODUCTION

In most fresh-water lakes of the higher latitudes of the temperate regions, winter brings about a set of conditions which differ sharply from those which prevail during the rest of the year. The ice cover, existing continuously for several weeks, and often blanketed by snow, rather effectively separates the body of water from the world above it, and makes it more certainly than ever a microcosm. Several otherwise normal processes are affected or suspended by this ceiling of ice and snow. Aeration of the water by the agitation of wind and wave is precluded, and exchange of gases with the atmosphere by bubbling and diffusion is greatly reduced. Heat exchange between air and water is interfered with, and the amount of transmission of light into the water becomes lowered, sometimes almost to the zero point.

The biotic consequences of these changed conditions are many and varied. The extreme stagnation that at times develops in the water may bring harm or death to countless organisms. Such a mortality, paricularly when it is of fish, is known as winter suffocation, or winter-kill.

Since winter-killing may occur frequently, it is perhaps not the most common cause of death of fish, nor that responsible in the long run for the greatest loss; but undoubtedly it is one of the most spectacular, as well as one of the most intensive. The appearance of piles and windrows of dead fish along the shores of a lake, at the breakup of the ice, is dramatic evidence of the harshness and suddeness with which the forces of nature can act. And when a considerable portion of the kill is made up of game and food fish, as it often is, the mortality assumes a serious aspect from the standpoint of fisheries management.

The significance and importance of the winter-kill problem was forcefully brought to the attention of those interested in Michigan fisheries by the extensive and heavy mortality which took place in 1935-36. During the winter of that year a considerable number of lakes in southern Michigan were affected, and hundreds of thousands of fish died. Scenes such as those shown in Figure 1 were common.

During that winter, the Michigan Institute for Fisheries Research carried out a certain amount of preliminary investigative and attempted rescue work. Experiments were performed in aeration of the water by pumping a stream of water into the air and allowing it to run back into the lake through holes chopped in the ice. In other experiments, long holes were cut through the ice, in the hope that atmospheric oxygen would enter the water through surface agitation.

These emergency aeration experiments met with little apparent success. However, the work of that winter emphasized the desirability of an extended

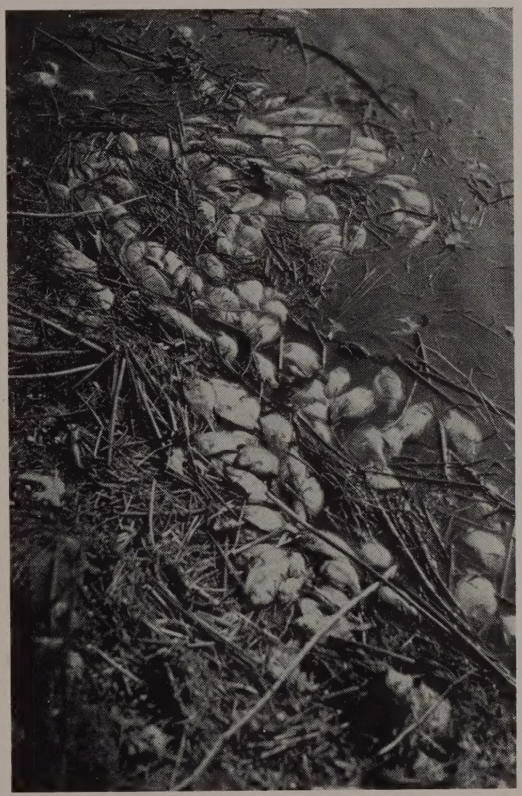

FIG. 1. Winter-killed fish, drifted along the shore of Green Lake after the breakup of the ice, 1936.

study of the winter-kill problem. Accordingly, the Institute arranged for such an investigation. The studies were carried out during the winters of 1937-38, 1939-40, 1940-41, and 1942-43, by the author, under the support of an Institute fellowship, and as a graduate research problem in the University of Michigan. This paper is a report on those studies, not only as they pertain directly to winter-kill, but also as they contribute to the knowledge of general limnological conditions in ice-covered waters.

Rather understandably, but none the less unfortunately, winter work in limnology and fisheries biology has been comparatively scanty in the past. The press of other duties, the difficulties of adapting apparatus and technique to work at freezing temperatures, and the physical hardships of winter weather have combined to keep many research workers indoors at a season when much useful and interesting information is to be found in the field.

ACKNOWLEDGMENTS

The investigation here reported could not have been performed without the generous assistance of many persons and agencies. Particular acknowledgment is given to the Institute for Fisheries Research, of the Michigan Department of Conservation, for financial support and for interest and encouragement, to A. S. Hazzard, its director, for able direction of the work, and to its staff and employees for assistance in many ways.

Gratitude is due to Professor Carl L. Hubbs, formerly of the University of Michigan, for help and guidance throughout the investigation. Helpful advice was received from many other faculty and staff members of the University.

The Associated Tackle Manufacturers, through a trust fund, provided substantial financial assistance to the work. Voluntary help in field work was received from several fisheries students at the University of Michigan.

HISTORICAL

There is little doubt that winter-kill of fish has been observed at various times for perhaps many centuries, since its occurrence is of a very striking nature. It is only within comparatively recent years, however, that very many references to winter fish deaths have entered the general biological literature. A few of these reported observations are cited.

Lühder (1871) described an instance of winter-kill in Germany in 1870-71. In 1871-72 a heavy mortality of fish took place in the Racine River, Wisconsin, where very large numbers of fish, including a large proportion of bass and pickerel, perished (Hoy 1872). Knauthe (1899) reported the winter-kill of many fish in certain artificially enriched carp ponds in Germany. In the Illinois River fish mortality in winter has occurred probably many times; it was recorded for the winter of 1894-95 by Kofoid (1903), and for the winter of 1924-25 by Thompson (1925), who stated that it is of common occurrence. Evermann & Clark (1920) recorded a winter death of fish in Lake Maxinkuckee, Indiana, some time during the period of their investigations there, 1899 to 1908. In Lake Yskjärvi, Finland, a "wholesale mortality" during the winters of 1915, 1922, and 1924 was reported by Jääskeläinen (1930).

In more recent years, winter-kill, sometimes of considerable intensity, has been reported from various places, some of which are: Massachusetts (Sweetman & Warfel 1936), Iowa (Aitken 1938, Sheppard 1938), Minnesota (Olson 1932, Smith 1941), and Utah (Higgins 1933).

The locations of the most serious instances of winter-kill in Michigan which have been satisfactorily reported for the period 1930 to 1941 are shown on the map of Figure 2. No accurate, dated records of kills prior to 1930 are available, although many oral communications from local residents indicate that heavy mortalities occurred in various lakes in winters of many years past.

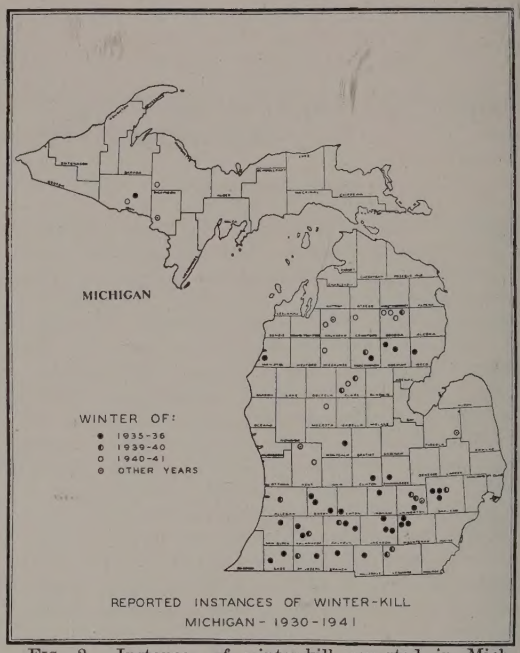

FIG. 2. Instances of winter-kill reported in Michigan, 1930-1941.

Many of the phenomena connected directly or indirectly with winter suffocations have been recognized and understoood, although sometimes rather imperfectly, by various previous workers. The literature contains a fairly large number of references to conditions in stagnant water under the ice, including some mention of the causes and effects of winter-kill. Although some of these writings are based upon actual observation, many others consist in large measure of hypothesis and conjecture, partially or wholly unsubstantiated. That many of these hypotheses later have been proved to be true is a favorable commentary upon the soundness of the original supposition. That others have been found to be unsound or even absurd points to the lack of information upon which they were based. One of the objects of the present study has been to obtain data which might contribute either to the proof or to the disproof of some of the theories and notions which have been proposed concerning the subject. A brief summary of some of these ideas follows.

The function of an ice cover in preventing aeration of the water by wind action is obvious. It was recognized by as early an author as Hoy (1872), and has been mentioned by numerous writers since. That ice, if it is thick or cloudy and especially if it is covered with snow, has another serious effect, in diminishing the transmission of light needed for photosynthesis, was understood quite clearly by Knauthe (1899). This effect has been reaffirmed by many authors: by Birge & Juday (1911), Olson (1932), Welch (1935),

Titus (1936), Aitken (1938), and Hubbs & Echmeyer (1938), to mention only a few.

The connection between winter stagnation and the abundance of organic materials in a lake has been pointed out by Drown (1892), Knauthe (1899), Welch (1935), and others; and various authors (Thompson 1925, and others) have called attention to the fact that critical conditions are more apt to obtain in shallow lakes than in deeper ones.

Most of the authors have assigned the primary blame for the winter death of fish to diminished dissolved oxygen content of the water, but several papers have mentioned other factors as being chief or contributing causes. Hoy (1872) stated that the death of many of the fish in the Racine River was "caused, probably, by the poison communicated to the water by the multitude of decaying minnows." Wickliff (n.d.) added to the lowered oxygen tension the presumed toxic effect of carbon dioxide, nitrogen, ammonia, and hydrogen sulfide. A popular point of view, expressed in the Milwaukee Sentinel (1939), referred to the "poisonous gases which mean death to the fish." In regard to the winter mortality of fish in acid bog waters, Jewell & Brown (1929) assumed the cause of death possibly to be either depletion of oxygen or the "production of toxic substances due to putrefaction."

WATERS INVESTIGATED

The major part of the field work of the present study was done on Clear Lake, Mud Lake, Green Lake, Bog Lake, and on a private farm pond, Pasinski's Pond, all in southeastern Michigan. These waters are listed in Table 1, and also are briefly described below. During part of one winter, Richmond Lake was under observation; also certain experiments, to be described later, were conducted in some small experimental ponds at the Drayton Plains state fish hatchery. Various other lakes in the southern peninsula of Michigan were used for occasional or single observations.

Clear Lake, Mud Lake, Bog Lake, and Green Lake lie within that part of Washtenaw and Jackson counties which has been designated the Waterloo Area, a region of generally poor farm land which was developed for several years by the U. S. Park Service as a recreational area. This area is in heavily glaciated territory, characterized by a rather rugged topography, abrupt transitions in soils types, and many and varied bodies of water. Within the Waterloo Area are several shallow lakes of the type which is apt to be subject to winter-kill.

Pasinski's Pond, in Livingston County, is also in a region of numerous lakes and pot-holes.

Table 1 gives some of the principal physical characteristics of the lakes studied. All of them, with the exception of the dystrophic Bog Lake, are in the eutrophic class, according to the Thieneman-Naumann system. Since eutrophic lakes vary greatly in organic richness, without sharp dividing lines, the lakes under study can be subdivided only in general, relative terms.

TABLE 1. Principal lakes studied; physical characteristics.

Lake	Area, Acres	Max. Depth, Feet	In Winter		Rooted Vegetation, Distribution	Methyl Orange Alkalinity, Usual range, p.p.m.	Class
			Inlet	Outlet			
Clear	140	35	No	No	Limited	150-180	Early-stage eutrophic
Mud	62	5	Yes	Yes	Widespread	200-260	Mid-stage eutrophic
Green	78	10	Yes	Yes	Widespread	170-210	Mid-stage eutrophic
Richmond	15	10	No	No	Widespread	140-160	Late-stage eutrophic
Pasinski's Pond	4	5	No	Yes	Total area	120-200	Late-stage eutrophic
Bog	1/4	6	No	No	Absent	5-10	Dystrophic

CLEAR LAKE

Clear Lake is surrounded by steep wooded hills, and has only a vague stream connection with any other body of water, receiving most of its water supply from surface and sub-surface run-in. Its morphometry is shown by the map (Fig. 3). The name of the lake is fully justified by the clearness of its water; a Secchi disc can be seen at 20 to 25 feet. There is considerable rooted vegetation in the shallower parts of the lake. The bottom contains a substantial proportion of marl. Compared to most of the lakes of the region, Clear Lake is relatively little advanced in eutrophy; in point of view of several characteristics, it is not far beyond the border-line between oligotrophy and eutrophy.

No winter-kill has ever been recorded for the lake. Hence it was included in this investigation as an example of those lakes of the general region which do not develop winter-kill conditions, so that comparative data might be secured which would demonstrate some of the difference between these lakes and lakes typically subject to winter-kill.

MUD LAKE

This lake, as shown by Figure 4, is uniformly shallow, with no water over about 5 feet deep. It is surrounded by wooded hills and grassy marsh. It normally has a flowing inlet and outlet. Thus there is somewhat of a current through the lake, modifying many of its conditions. Otherwise its characteristics are rather typically those of many southern Michigan lakes. The water is moderately clear. Much of the bottom is composed of soft, organically rich material, with some marl areas. The lake produces a reasonably large amount of fishing for largemouth bass and panfish.

GREEN LAKE

The size, shape, and depth of Green Lake, and the location of sampling stations, are shown by Figure 5. The lake has a small but steady inlet, which carries seepage water from a large marsh. Most of the lake is shallow, less than 10 feet deep, with dense rooted vegetation.

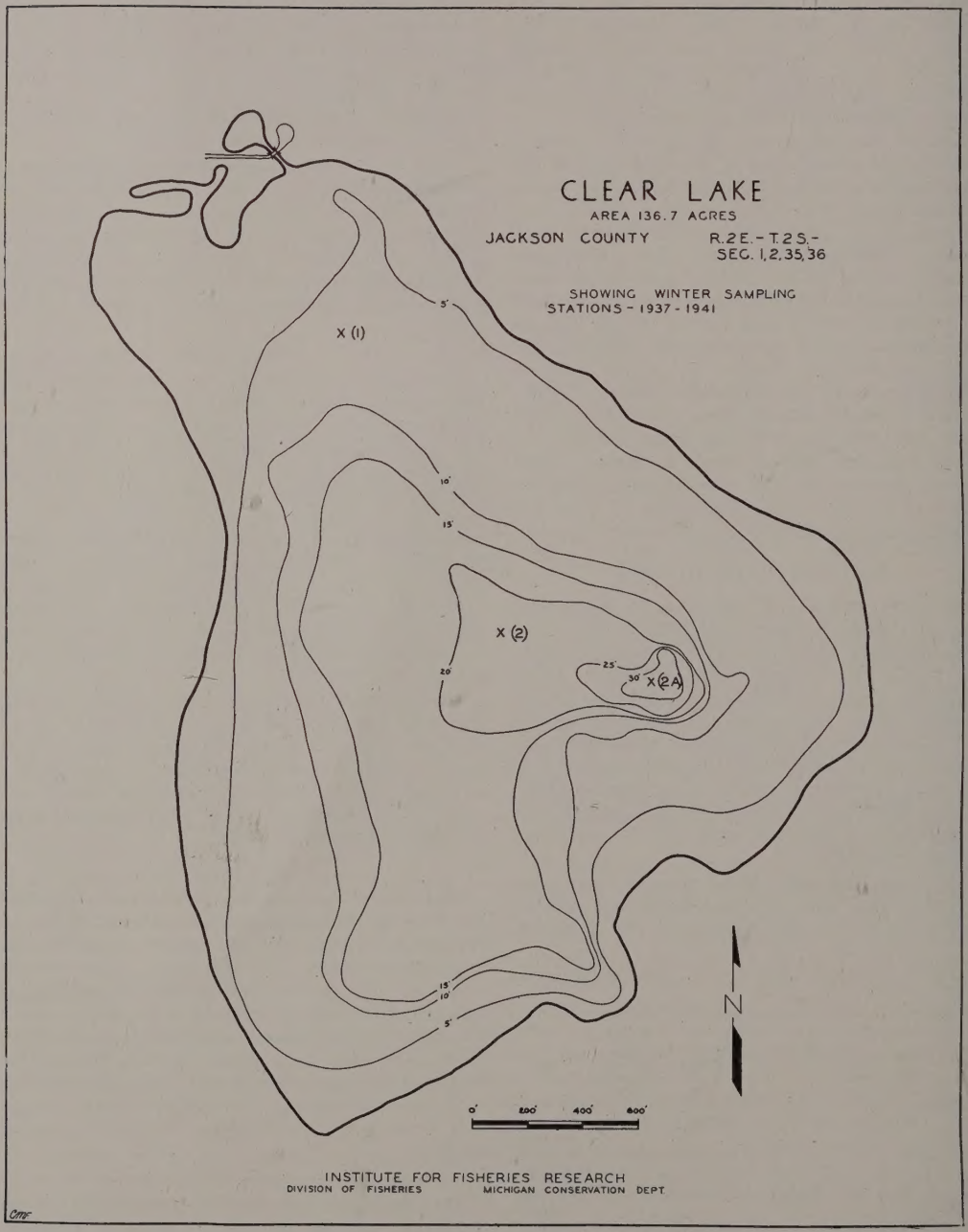

FIG. 3. Clear Lake. Sampling stations indicated by x ( ).

FIG. 4. Mud Lake. Sampling stations indicated by x ( ).

The lake is semi-artificial, being enlarged a few years ago by the construction of an earth dam. The newly flooded bottom as well as that of the original basin, is very rich in organic material. The lake has suffered severe winter-kill of fish in several years. However, it has retained or been artificially restocked with a sufficiently large population of game fish to provide good fishing.

BOG LAKE

The small pot-hole here called Bog Lake is a typical brown-water acid bog lake. No map is available. The lake is about ¼ acre in size, and oval in shape. At its present level, it is isolated from any other body of water; but at the slightly higher level which probably existed at some time in the past, it had an outlet. Its greatest depth, 6 feet, prevails over most of its area, since the slope of the shore is abrupt.

Bog Lake fits quite well the general conception of a lake of the dystrophic type, and conforms well to the definition given by Welch (1935) for a bog lake. Its water is stained a dark brown, is very soft, and moderately acid. The bottom material is gelatinous and flocculent, although there is not a false bottom such as that which occurs in many bog lakes. The only species of fish known to live in Bog Lake is the mud minnow, *Umbra limi*. Nothing has been recorded concerning possible winter-kill of fish in this lake.

PASINSKI'S POND

This private pond was constructed about 1932, by damming a natural valley. It has no inlet, but receives surface drainage from grassy hillsides, and is fed by underground seepage. A small motor-driven pump on the east shore of the north end of the pond, capable of delivering approximately 60 gallons per minute from a shallow well, is used at times to help maintain the water level. There is a small outlet which flows except at times of drouth.

As shown by the map, Figure 6, the pond has an area of about 4 acres, and a maximum depth of 5 feet. Its soft bottom has a high organic content. The water is choked with rooted water plants, the bulk of which consists of the waterweed, Anacharis. There is also a considerable amount of filamentous algae, most of which apparently is Spirogyra. The amount of algae present in a growing condition varies

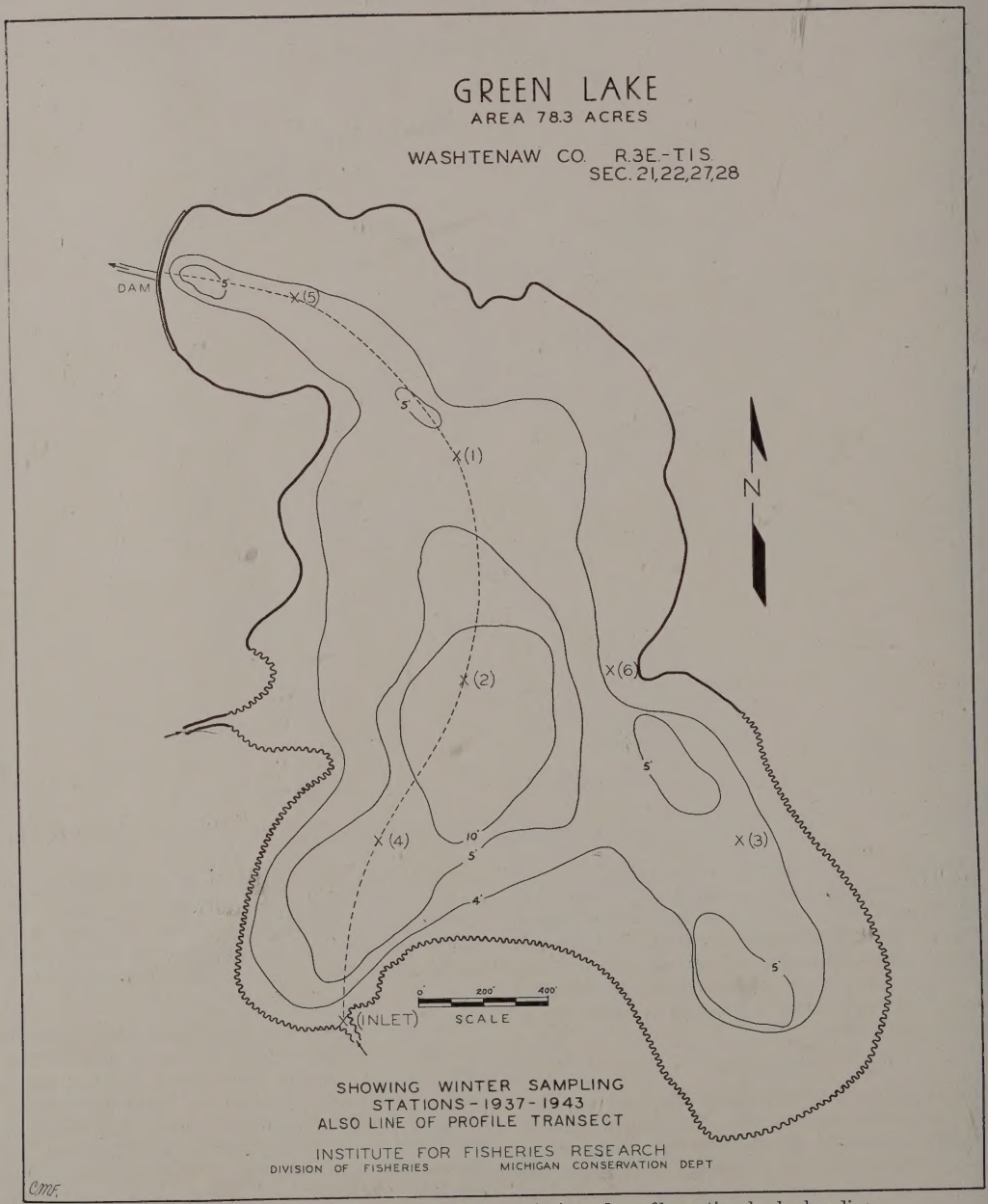

FIG. 5. Green Lake. Sampling stations indicated by x ( ), and profile section by broken line.

from one time to another, but is nearly always greater in the end of the pond nearest the outlet (the south end) than in that nearest the pump (the north end).

The pond has been the site of various activities of the Institute of Fisheries Research. It was poisoned in 1937 and 1938, in an attempt to destroy the abundant population of bullheads, *Ameiurus nebulosus*, which was then the only species of fish present. Large numbers of bullheads were killed, but an unknown number survived. The pond was stocked, in 1938, with bluegills.

In the winter of 1939-40 a heavy winter-kill took place in the pond, apparently totally destroying the bluegill population, and killing many bullheads. Winter-kill in previous years has been reported, and in the summer of 1937 a large number of fish were reported to have died because of summer stagnation.

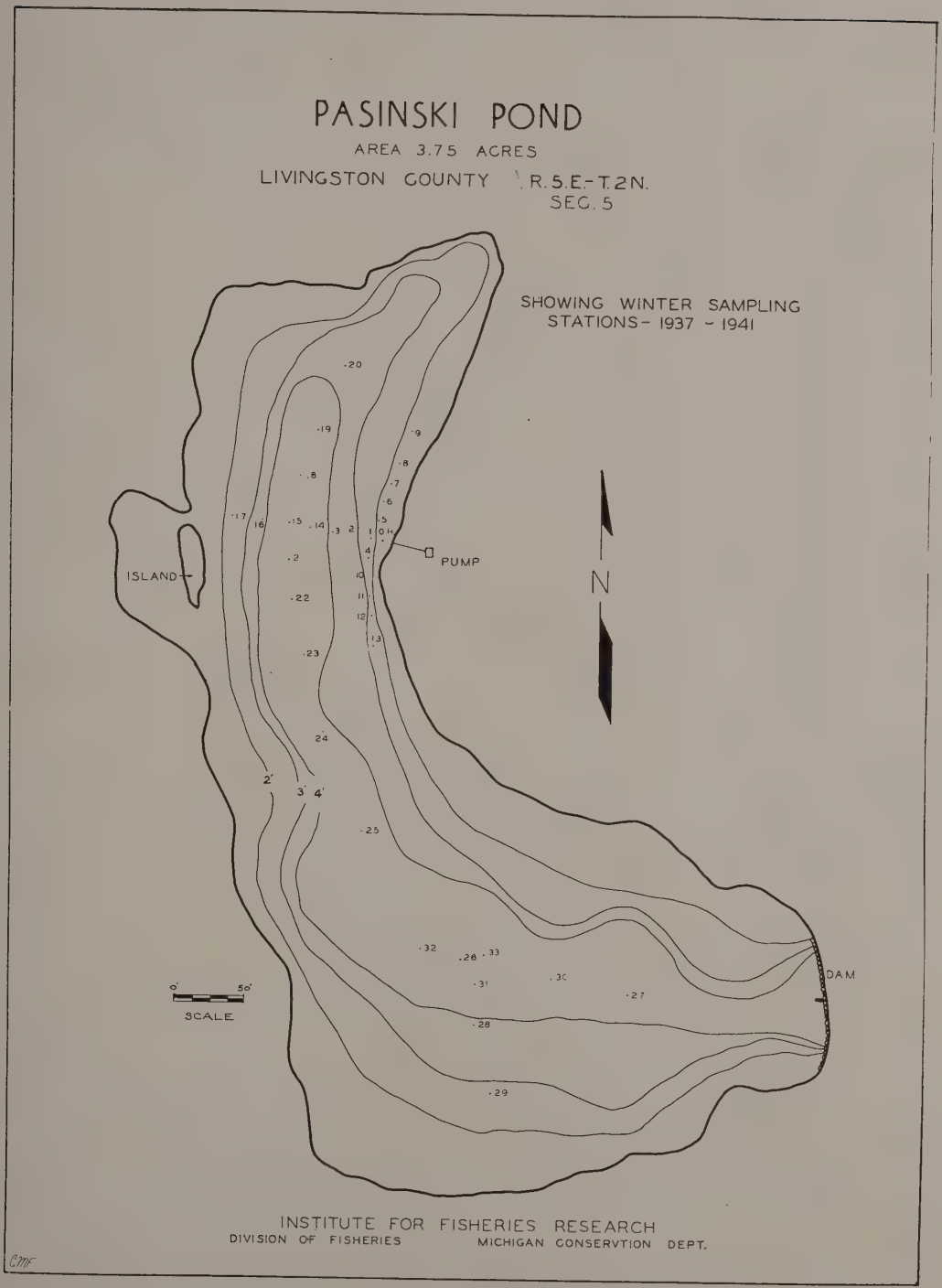

FIG. 6. Pasinski's Pond. Sampling stations numbered.

RICHMOND LAKE

Richmond Lake is a small, shallow lake, extremely rich in organic materials, with a bottom of soft mucky material, which at times becomes putrescent. The lake apparently is filling in rather rapidly, and already may be considered to be well advanced in senescence.

The lake was studied only in the winter of 1939-40, and at a time when serious conditions already had developed. There was a considerable loss of fish that winter. Nothing is known concerning previous winter-kills.

HATCHERY PONDS

For some experiments described below, three small experimental ponds at the Drayton Plains hatchery were used. These ponds are entirely artificial and are very nearly alike. Each is 50 by 100 feet, with a fairly uniform depth of 3 feet. The bottom is soft mud, and the rooted vegetation is limited. The ponds may be filled with water from the Clinton River, and they have overflow outlets.

PROCEDURE, METHODS, AND EQUIPMENT

SAMPLING STATIONS

During the course of the investigation, a large number of sampling stations were established. Some of these were used continuously throughout the study, some for only one or two winters, and some only once or a few times.

In Clear Lake, a shallow station (Station 1) and two deeper ones (Stations 2 and 2a) were used.

The original Station 1 of Mud Lake was used in three winters. In two of these winters, samples were taken from three other stations and from the inlet and outlet streams.

Likewise in Green Lake the original Station 1 was sampled throughout the study, and for some of the work other stations, including Stations 2 and 4 in deeper water, were used. In the winter of 1939-40, a hole in the ice, a few feet across, was artificially kept open for a few weeks.

Locations of the various stations on Clear, Mud, and Green Lakes are shown on the maps of Figures 3-5.

In Pasinski's Pond, Station 15 in the north end, and Station 26 in the south end, became the principal routine sampling stations, but for some experimental work on the pond in 1939-40, described below, over 30 additional stations were used. These are shown on the map of Figure 6. The open hole of 1939-40 was near the point of discharge of the pump.

The depths of sampling were not entirely constant. They were affected somewhat by variations in lake water level, and by slight changes in station location. Although the stations were marked with stakes set into the ice, their exact positions changed slightly from time to time, and of course varied somewhat from winter to winter.

The primary sampling depth at each station was that designated as "surface" or "top." This sample was taken at from 4 to 6 inches below the surface of the water as it stood in the hole chopped through the ice. Although this level at times may have been above the under surface of the ice, it is assumed that it held water which previously had been just under the ice, and which had flowed into the hole.

The sample of next importance at any station came from about ½ to 1 foot above the bottom, this level being the deepest at which the sampler could be operated without stirring up the bottom materials. This sample is called "bottom." At many stations, samples also were regularly taken at various intermediate depths.

SAMPLING

The lakes were sampled periodically, each winter, throughout the entire period when the ice was safe to walk on. Whenever the ice was thick enough to permit doing so, an automobile was driven onto the lakes. At other times either a portable shanty or a specially fitted hand sled was used. Both the shanty and the sled were equipped with gasoline lanterns to prevent water samples from freezing.

The hole for sampling was made beside the station marker, or at a short distance, where average conditions of ice and snow existed. The hole, from 8 to 10 inches in diameter, was cut with a steel ice-spud, and care was used to minimize the agitation of the water by upwelling.

Samples of water were taken with a sampler modified somewhat from that figured in Standard Methods (American Public Health Association 1936, p. 140). The sampler consists of a metal can, in which the sample bottle sits, with tubes for delivery of water and escape of air, so arranged that the volume of water in the bottle is displaced at least three times, without the entrainment of air bubbles. For winter work, this sampler was found to be superior in many respects to the Kemmerer bottle. It is much less subject to freezing, and it is more sturdy and can better withstand handling under the ice. Since it is more compact, it can take a sample from a thinner stratum of water, and from nearer the bottom.

When samples were taken at more than one depth at a station, an almost unvarying procedure was employed. The sample from the surface was taken first, followed by that from the next lower depth, and so forth. Thus no layer of water was subjected to agitation, by air bubbling from below it or by the sampler passing through it, before a sample from that layer had been secured.

Water samples were collected in 250-ml., ground-glass stoppered bottles. They were prevented from freezing, but were kept at a low temperature until their analysis had been completed.

DISSOLVED OXYGEN

Dissolved oxygen was determined in 1937-38 by the Rideal-Stewart modification of the Winkler method. This modification is extremely tedious at near freezing temperature, so in later winters the rapid modification of the Winkler method, for waters containing organic matter (Standard Methods 1936, p. 145), was used. The procedure up to and including acidification was

carried out in the field, sometimes at the station, but more often after the sample had been taken to shore. At low temperatures, it is likely that no significant change in the dissolved oxygen content of water in a tightly stoppered bottle takes place in an hour or two (Birge & Juday 1911, p. 17). The samples were titrated, after transportation to the laboratory, within a few hours and without having been allowed to warm up.

Results of the dissolved oxygen determinations are expressed in parts per million (p.p.m.). It is probable that this expression has a more significant meaning than does percent saturation. At any rate, since the temperature of the water under the ice stays within rather narrow limits, the two sets of figures are closely proportional.

pH, Carbon Dioxide, Alkalinity

The pH was measured colorimetrically, using a spot-plate, pipette type pH set. Free carbon dioxide was determined by titration with standard alkali in the presence of phenophthalein indicator. Total alkalinity (methyl orange alkalinity) was measured by titration with standard acid, using methyl orange as an indicator.

Biochemical Oxygen Demand

Biochemical oxygen demand was determined by constant temperature incubation in 250-ml. ground-glass stoppered bottles. The method used was that of the U. S. Public Health Service (Theriault 1927, American Public Health Association 1936), with considerable modification and simplification. Undiluted samples were used whenever possible; when dilution was necessary, the preference in calculating weighted mean values was given to the sample least diluted. A dilution of 1:2 often sufficed, and the greatest dilution necessary, even with samples having a high oxygen demand, was 1:5. All dilutions were made with aerated distilled water, without bacterial seeding. Since the dilutions were not great, it is rather probable that sufficient bacteria, as well as inorganic nutrients, were supplied by the water sample. All the results are expressed in parts per million.

B.O.D. measurements were made at two incubation temperatures; at the standard temperature of 20° C., giving results that may be compared with those of other investigators, and at 0° C. (rather, just above 0°), which temperature closely simulates natural conditions under the ice. Incubation at 20° was performed in an electric incubation, and at 0° in a household electric refrigerator. Most of the samples were incubated for the standard 5-day period; but one series was incubated for 60 days.

Light Penetration

Measurements of the penetration of light through water, ice, and snow were made with a specially designed submersible photometer, employing photoelectric cells. In recent years this type of photometer has come into rather common use, particularly in oceanography. Many different designs have been employed (Ellis, 1934, Pearsall & Ullyott 1933, Burr & Burr 1934, Utterback & Wilson 1940, etc.). All, however, embody photoelectric cells of the selenium rectifier, or similar, type. They differ mainly in external design.

The photometer used here (see Figures 7 and 8) was built with special adaptations for use under ice.

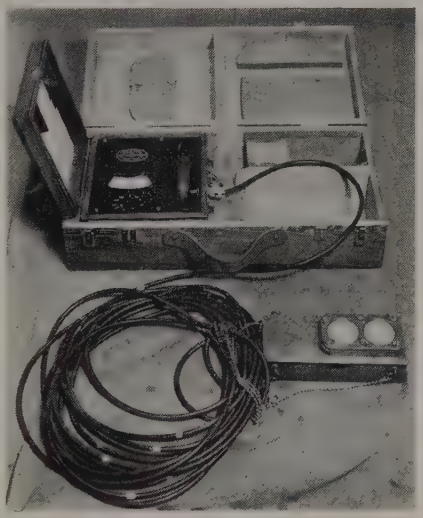

Fig. 7. Submersible photometer, with cable and microammeter.

It consists of a suitably housed receiver, using two Weston "Photronic" cells, and connected by a waterproof cable to a very sensitive multiple-range galvanometer. The brass housing case of the receiver can be fitted with a detachable pipe handle, enabling it to be thrust under the ice to a distance of about two feet from the edge of the hole which must be cut into the ice. With the handle removed, the receiver can be lowered and raised by means of the electric cable. In general principle, the apparatus is similar to that described by Zinn & Ifft (1941), but differs in mechanical design, and in using an extra Weston cell for added sensitivity. In optical and electrical detail, it meets the chief specifications of the International Council for the Exploration of the Sea (Atkins et al. 1938).

Between the cells and the water there is, first, a plate glass window, and above that a removable diffusing window made of single opal-flashed glass. The space between the two glasses may contain an interchangeable glass color filter. Also in this space may be inserted a light-reducing filter for cutting down the intensity of light on bright days, so that the readings are not off the scale of the meter. The filter so used for this investigation was made of exposed and developed photographic film (a glass filter would be more durable).

Color filters of three wave-lengths were used, approximating very closely the specified ranges of

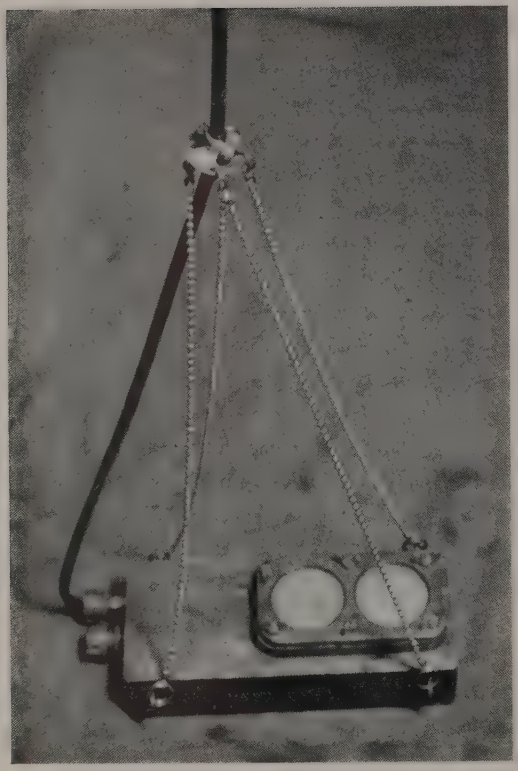

FIG. 8. Target of submersible photometer, showing method of suspension by electric cable.

green red, and blue, as given in Atkins et al. (1938). These colored glasses were obtained from the Corning Glass Works.

The procedure of making measurements of light penetration through ice and snow was as follows. An initial reading was made with the receiver in the air, resting horizontally on the surface of the ice. In recording the data, this reading was termed "air." Then, with as little loss om time as possible, the receiver was thrust under the ice, with the upper face of the receiver held tightly and flatly against the under surface of the ice, and a reading was taken. In the data tabulation, this reading is called "ice." Another reading was taken in the air, another under the ice, and so forth, sufficient alternating readings being made to make sure that the intensity of daylight had remained reasonably constant throughout the process. If measurements at various depths in the water also were made, the same alternating procedure was followed.

It was found that on either completely cloudless days or heavily overcast days the light remained sufficiently constant to provide acceptable results over periods long enough to make the necessary number of readings, and that only times when the sky was partly cloudy needed to be avoided. Utterback (1933), however, found that at certain times "the intensity of the visible light may vary within a few minutes by several percent, even though there be a cloudless sky and a clear atmosphere." Hence, although considerable precaution was used, it is not impossible that a small error may have entered the results obtained. Measurements were always made at about the same time of day, usually close to noon, to avoid large changes in the angle of light.

Measurements of penetration of light through the snow cover were, of necessity, made indirectly. The penetration through the ice plus snow was measured. Then the snow was removed, and a measurement made of penetration through the ice alone. From these two readings the amount of penetration through the snow alone was computed.

The instrument was calibrated in terms of light intensity in foot-candles incident upon the face of the target, by the use of a standardized photoflood bulb. The temperature correction was ascertained by calibration at several temperatures. It was found, in agreement with the statement of Utterback & Wilson (1940), that the temperature correction is greater at higher illumination levels.

The results are expressed in terms of percentage penetration. This figure is obtained by dividing the amount of light which penetrates through a given layer of ice, snow, or water, by the total amount of light impinging upon that layer. It must be remembered that both these figures, as measured by a photronic cell, are not true total light, since this cell has a maximum sensitivity in the yellow-green portion of the spectrum.

Possible error caused by the loss of low-angle light was not taken into account. Such loss is minimized by the opal glass diffusing window. Furthermore, the various readings are comparable, since the angle of light always was approximately the same.

RESULTS AND DISCUSSION

WEATHER, ICE, AND SNOW

The winter climate of southeastern Michigan is moderately cold, with fairly even precipitation. Snows are apt to be frequent, but rather light. Many days are cloudy or partly cloudy, and there is fair to moderate humidity. There are many winter breezes and light winds, but rarely is there a storm of blizzard-like intensity. Midwinter thaws are frequent, and it is rather seldom that snow remains on the ground continuously throughout the winter.

The time of freezing-over of the lakes in the region not only varies with the size, depth, and exposure of the lake, but also varies greatly from year to year. In the winter of 1937-38 there was an ice cover on some of the lakes studied from December 10 to March 15. In 1939-40 the ice cover did not form until almost January 1, but it lasted until April 5. In 1940-41 the lakes froze over early, some of them being completely covered by December 5. A warm spell in late December partially opened up the lakes for a few days, from December 25 to January 5.

TABLE 2. Thickness of ice and snow on lakes studied.

Lake	Date	Ice, inches	Snow	
			Inches	Condition
Green...	Dec. 11, 1937	...	Trace	...
	28	8	None	...
	Jan. 5, 1938	9	None	...
	12	9	1	...
	19	10	1	Crusted
	26	12	Trace	...
	Feb. 2	12	None	...
	9	5	None	...
	20	3	Trace	...
	27	2	3	Slushy
	Mar. 8	2	...	...
	Jan. 10, 1940	5	2	...
	17	5	½	...
	24	10	1	...
	31	10	2	...
	Feb. 8	10	3	...
	14	10	3	...
	21	...	2	Crusted
	28	...	6	...
	Mar. 8	14	2	Crusted
	11	14	1	...
	16	14	½	New
	20	12	3	New
	23	...	3	Crusted
	27	12	5	...
	31	8	...	...
	Apr. 3	6	None	...
	Dec. 10, 1940	4	None	...
	17	6	Trace	...
	21	5	None	...
	24	3	None	...
	Jan. 1, 1941	Open	...	...
	7	4	None	...
	12	6	1	...
	23	8	None	...
	26	8	None	...
	28	10	1½	...
	Feb. 9	10	2	Dry
	14	6	None	...
	24	10	2	Drifted
	Mar. 2	10	1	Drifted
	4	10	½	Drifted
	8	10	Trace	...
	Dec. 5, 1942	3	None	...
	16	6	½	...
	23	9	1	Crusted
	29	6	None	...
	Jan. 4, 1943	8	2	Dry
	8	8	3	Drifts, plus new
	12	8	3	Dry, firm
	16	9	6	Drifts, plus new
	22	12	10	Dry, over slush
	24	12	Trace	...
	29	12	Trace	...
	Feb. 2	12	1	New, crusted
	5	...	Trace	Nearly gone
	8	12	1	Crusted
	13	12	½	New
	22	12	None	...
	27	10	None	...
Mud....	Dec. 11, 1937	4	Trace	...
	28	6	None	...
	Jan. 5, 1938	...	None	...
	12	8	1	...
	19	12	...	...
	26	12	Trace	...

TABLE 2 (continued)

Lake	Date	Ice, inches	Snow	
			Inches	Condition
	Feb. 2	12	None	...
	9	7	None	...
	20	4	Trace	...
	27	4	4	...
	Mar. 8	3	None	...
	Jan. 6, 1940	4	1½	...
	10	5	2	...
	13	5	2½	Slushy
	17	6	½	...
	20	8	½	...
	24	10	1	...
	28	12	1½	...
	31	10	2	...
	Feb. 3	10	3	...
	8	10	3½	...
	11	...	...	...
	14	10	3	Packed
	18	12	2	Packed
	21	12	2	Crusted
	25	...	2	...
	28	...	6	...
	Mar. 3	...	2	Slushy
	8	12	1	Crusted
	11	12	1	...
	16	12	2	...
	20	10	3	New
	23	12	3	Crusted
	27	12	5	...
	31	8	...	...
	Dec. 10, 1940	4	None	...
	19	6	Trace	...
	24	4	None	...
	Jan. 1, 1941	Open	...	...
	7	3	None	...
	14	6	1	Crusted
	23	6	None	...
	30	8	1½	...
	Feb. 4	10	None	...
	11	10	1½	...
	23	10	1	...
	Mar. 2	10	1	Drifted
	8	10	Trace	...
Clear...	Dec. 28, 1937	10	None	...
	Jan. 5, 1938	10	None	...
	12	10	1½	...
	19	12	...	...
	26	12	Trace	...
	Feb. 2	12	None	...
	9	10	None	...
	20	5	Trace	...
	27	4	3½	...
	Mar. 8	2	...	...
	Jan. 6, 1940	4	1½	...
	10	6	2	...
	13	6	3	Slushy
	17	8	½	...
	20	9	½	...
	24	12	1	...
	28	14	1½	...
	31	12	2	...
	Feb. 3	12	3	...
	8	12	4	...
	11	12	6	...
	14	12	3	Packed
	18	12	2	Packed
	21	12	2	Crusted

TABLE 2 (continued)

Lake	Date	Ice, inches	Snow	
			Inches	Condition
	25	14	3	...
	28	...	6	Crusted
	Mar. 8	14	1	Crusted
	11	14	½	...
	16	14	2½	...
	20	14	3	New
	23	14	3	Crusted
	27	14	5	...
	31	10	None	...
	Apr. 3	8	None	...
	Dec. 10, 1940	1	None	...
	15	...	None	...
	21	6	None	...
	Jan. 1, 1941	Open	...	..
	7	Thin	None	...
	12	8	1	...
	23	6	None	...
	30	10	1½	Crusted
	Feb. 6	10	None	...
	14	8	None	...
	23	...	1½	Drifted
	Mar. 2	10	1	Drifted
	8	10	Trace	...
	13	6	...	Melting
Bog.....	Jan. 6, 1940	2	2	...
	13	3	3	Slushy
	20	4	½	...
	28	5	2	...
	Feb. 3	5	3	...
	11	4	4	Slushy
	18	4	1	Packed
	25	4	3	...
	Mar. 11	4	½	...
	16	5	½	New
	23	4	3	Crusted
	27	6	5	...
	Dec. 10, 1940	2	None	...
	17	3	Trace	...
	21	3	None	...
	Jan. 1, 1941	Thin	...	..
	7	2	Trace	...
	14	3	1	...
	23	4	None	...
	28	5	1½	..
	Feb. 4	5	½	...
	11	6	2	...
	16	6	½	New
	25	10	2	Crusted
	Mar. 2	8	1½	Crusted
	4	8	½	New
	10	9	...	Hard
	27	6	None	...

After refreezing, the ice remained intact until almost April 1. In the winter of 1942-43 the ice seal lasted from December 1 until after March 20.

Table 2 gives the thickness of the ice on the various lakes of the survey, on the dates on which these lakes were visited. These figures represent, usually, the average thickness over the surface of the lake.

Also given in Table 2 is the depth of snow on the ice from time to time. Obviously, only an approximately average figure can be given, because drifting often caused the snow to be much deeper in some places than in others.

Figure 9 shows the depth of snow throughout the periods of ice cover of the winters 1935-36, 1937-38, 1939-40, 1940-41, and 1942-43. The data of Table 2 were obtained at too infrequent intervals to be adequate for the construction of smooth curves. Therefore they were supplemented by data, secured from the weather station of the University of Michigan, for the amount of snow on the ground, from day to day, in Ann Arbor. Snowfalls in the region usually are general, and the depth of snow tends to be approximately the same (except for drifting) from one place to another.

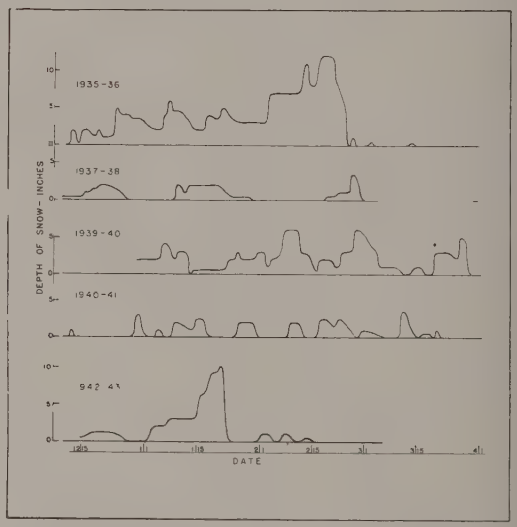

FIG. 9. Depth of snow on the ground in the area studied, during the periods of ice cover.

It is readily apparent from Figure 9 that in the year of the heavy winter-kill, 1935-36, not only was the snow fairly deep, but it remained on the ice for a long uninterrupted period. Likewise in 1939-40, a winter with some kill, although the snow was not so deep, it covered the ice for a rather long unbroken span of time.

In contrast, in the winter of 1937-38, and even more so in 1940-41, the snow on the ice frequently was dissipated by thaw or rain; and hence, although there were many snowstorms, there were no extended periods of snow coverage. These two winters were virtually free from winter-kill in the lakes in the region.

In the winter 1942-43 snows began early, and as the result of one snowfall after another the ice (on Green Lake) by January 20 was covered with 10 inches of snow. At this time much of this snow had become slush, because of melting and of the presence of water on the ice.

Rather suddenly, probably within the space of one night, the ice was lifted, apparently by a change in the water level of the lake combined with the buoyancy of the ice. The water on the ice flowed through

cracks and around the ice sheet, and that part of the slush remaining on top of the ice soon froze into a layer of rough, cloudy ice. The ice was covered with snow only for brief periods throughout the rest of the winter.

It is highly probable that this sudden disappearance of the snow on Green Lake happened just in time to prevent a serious winter-kill, for conditions in the water were fast becoming critical.

WATER TEMPERATURE

Water temperature measurements were made regularly only in one winter. Some general trends were noticed. One evident tendency is toward the development of a very abrupt drop-off in temperature in the upper few feet of water, with a much more gradual decline from there to the bottom. Another is the distinct warming up of the general mass of water as the winter season progresses. Probably an insignificant part of this increase in temperature is due to the oxidation of organic matter, virtually all of it being produced by the radiant energy of sunlight. The occasional entrance into a lake of a considerable amount of comparatively warmer rain water may contribute a small part of the heat.

DISSOLVED OXYGEN

By far the best single indicator of conditions for fish life in the water under the ice is the amount of dissolved oxygen. The determination of dissolved oxygen is a relatively simple and reliable procedure, and one which is capable of adaptation to winter field work. Therefore the data of this study contain a large proportion of dissolved oxygen values.

A relatively large range of dissolved oxygen values was observed, at various times and places. A few of the highest oxygen readings recorded during the survey were: Clear Lake, 16.2 p.p.m., Station 1 on January 20, 1940; Mud Lake, 19.4 p.p.m. (approximately 135 percent saturation), at Station 4 on March 11, 1940; Bog Lake, 21.0 p.p.m. (about 145 percent saturation), on February 11, 1941; and Pasinski's Pond, 28.0 p.p.m (about 190 percent saturation), at Station 26 on January 31, 1941. During the winter 1940-41 a considerable number of samples from Pasinski's Pond contained over 20 p.p.m. dissolved oxygen.

The most rapid increase in oxygen noted was in Green Lake, at Station 5 at the surface, where the oxygen changed from 1.8 p.p.m. on February 5, 1943, to 9.8 p.p.m. on February 8, an increase of 8.0 p.p.m. in 3 days, or at the rate of 2.7 p.p.m. per day. The most abrupt decline noted was in Pasinski's Pond, at Station 27. Here the oxygen fell from 12.3 p.p.m. on February 12, 1940, to 2.4 p.p.m. on February 14, a decrease of 9.9 p.p.m. in two days, or at the rate of 5 p.p.m. per day.

The oxygen in Clear Lake showed considerably less variation (Figs. 10 and 11) than that in the more shallow, more eutrophic lakes. At Station 1, in Clear Lake, the top and bottom samples were remarkably similar in oxygen content at nearly all times. At the deeper Station 2 (Station 2a in 1940-41) a much more evident stratification was found. The water layers at the surface, 10-foot, and 20-foot levels had an almost uniform content of dissolved oxygen at the start of the winter of 1939-40, but gradually developed the spread in oxygen values typical of stratification (Fig. 10). Strangely enough, in the winter of 1940-41, the oxygen in the deeper water was rather low even at the onset of the ice cover; the oxygen curves for this station in Figure 11 are almost level throughout the winter. Apparently for some reason stratification already had developed before the first samples of that winter were taken (even though sampling was started two weeks earlier than in the preceeding winter). It is possible, although not definitely known to be the case, that following the fall overturn some sort of an oxygen demand (more or less pronounced and rather immediate) developed in the lower water, and that this demand was sufficient to bring about such early stratification.

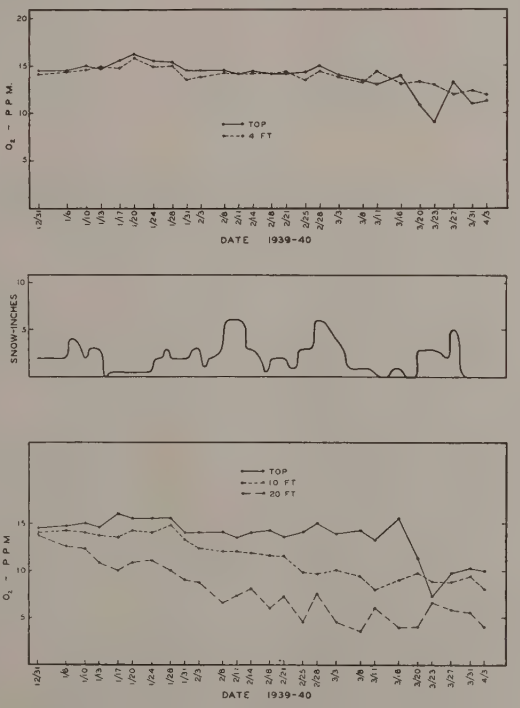

FIG. 10. Dissolved oxygen and snow cover, Clear Lake, 1939-40. Upper curves are for Station 1, lower ones for Station 2.

The greater eutrophy of Mud Lake is reflected in its oxygen curves for 1939-40 (Fig. 12). As may be seen by juxtaposing these curves with the curve which represents depth of snow, there was a definite response in the oxygen value—especially at some stations—to changes in light intensity. Stations 2, 3, and 4 showed low oxygen during the period of snow

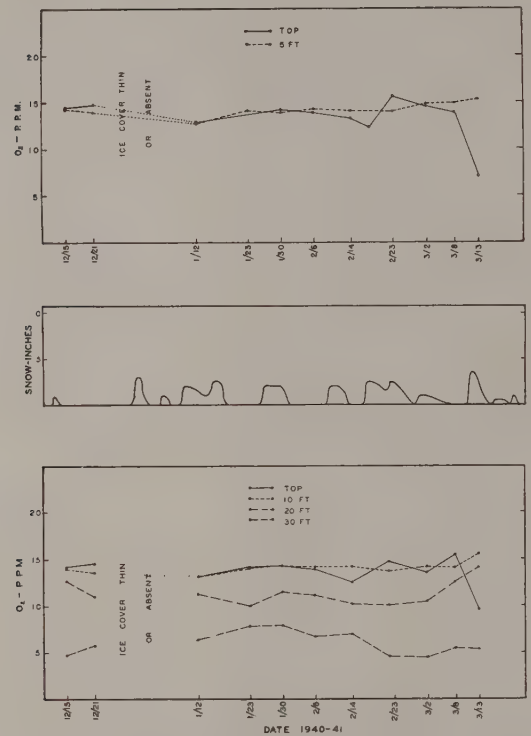

FIG. 11. Dissolved oxygen and snow cover, Clear Lake, 1940-41. Upper curves are for Station 1, lower ones for Station 2a.

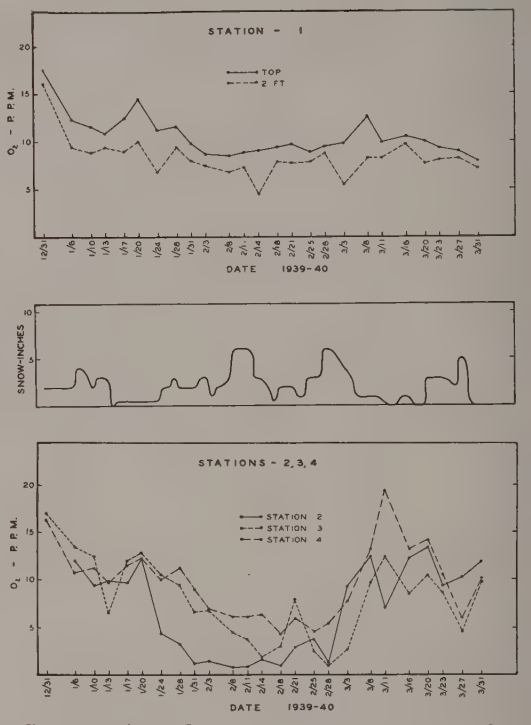

FIG. 12. Dissolved oxygen and snow cover, Mud Lake, 1939-40. The curves for Stations 2, 3, and 4 are for surface samples.

cover throughout most of February, and very sharp rises in oxygen in early and mid-March, when the snow was light or absent. These three stations, which initially were chosen on the basis of differences in vegetation and bottom materials, failed to show many significant differences in dissolved oxygen values, the most evident one being that the oxygen at Station 2 (which had a soft marl bottom) for some reason dropped to a low value much sooner than did that at the other stations.

Station 1 was more or less directly in the path of flow of water crossing the lake, and hence its oxygen curves showed less response to changing light conditions, because of the steadying influence of the inflowing water. However, it is of interest to note that, in spite of the current, a definite stratification existed at this station, the bottom water always containing less oxygen than the surface water. The inflowing water itself scarcely could have been stratified, since the stream was shallow; therefore even a transitory stay in the deep part of the lake was enough to bring about a distinct stratification.

In 1939-40 the outlet water on Mud Lake almost continuously had less dissolved oxygen than did the inflowing water (Fig. 13). In 1940-41 exactly the reverse condition existed. In other words, during the one winter the water lost oxygen during its stay in the lake, in the other winter it gained oxygen. It is evident that this difference came about not so much by any shift in the curve for the inlet water from one year to the next, as by a vast change in the curve for the outlet. The correlation with the respective conditions of snow cover and light for the two winters is evident.

Curves are given for only one station in Green Lake (Figs. 14 and 15), since this station fairly well typifies the lake. Here again the relation between surface and bottom water is evident. The curve for the bottom follows closely that for the top, but almost constantly remains below it. This relationship, repeated over and over for various lakes and stations, can lead logically to only one line of reasoning. The two levels of water are subject to the same influences, light on the one hand and oxygen demand on the other, but to different degrees. The bottom water either receives less light and hence produces less oxygen, or is subject to greater oxygen demand and hence loses more oxygen,[1] or both; therefore the oxygen curve for the bottom water falls below that for the surface water. With such a difference, however, the two curves should become progressively

[1] It may be well to take into account the difference in temperature (usually almost 4° C.) between the top and bottom, with perhaps a consequent difference in metabolic activity of the contained organisms.

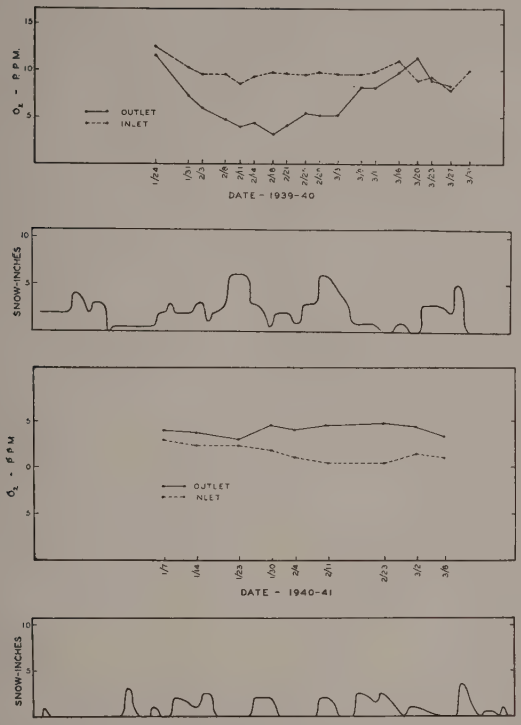

FIG. 13. Dissolved oxygen and snow cover, Mud Lake. Inlet and outlet, 1939-40 and 1940-41. Surface samples.

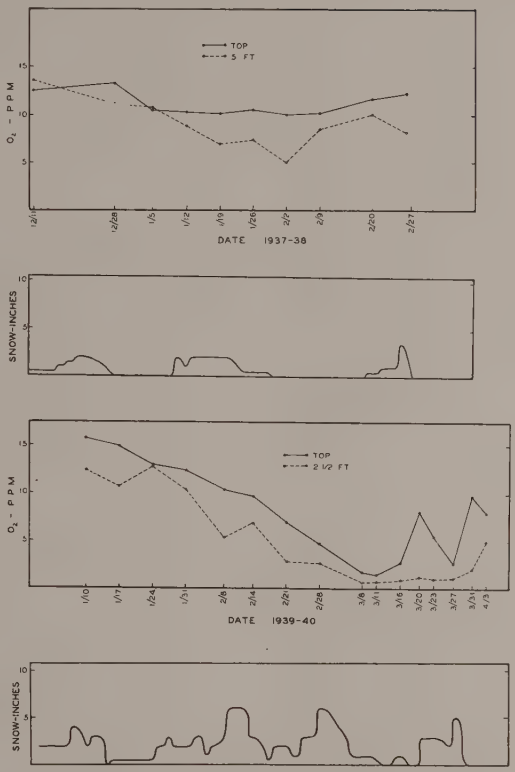

FIG. 14. Dissolved oxygen and snow cover, Green Lake, Station 1, 1937-38 and 1939-40.

more divergent throughout the winter (as in the case of the deeper station in Clear Lake in 1939-40), instead of following each other so closely. For some stations, it seems as if almost as much divergence between the curves exists at the start of the winter as later, and that the curves tend to be roughly parallel. In other words, this is more evidence that stratification may take place, and quite rapidly, even before the ice forms, as is postulated above for the deep station in Clear Lake in 1940-41.

In respect to the amount by which the bottom water at a shallow station may remain lower in oxygen throughout the winter than the surface water, an interesting series is presented in the curves for the several lakes, starting with Clear Lake (Figs. 10 and 11), and progressing through Mud Lake, Green Lake, and Pasinski's Pond (Figs. 12, 14, 15, and 17), to Bog Lake (Fig. 16). In Clear Lake the oxygen was practically the same at the two depths (at Station 1); for Bog Lake the values were widely separated. Yet the tendency, discussed above, for the lower curve to parallel the upper one existed to some extent even in Bog Lake.

Green Lake (Figs. 14 and 15) offers another example of the readily apparent connection between depth of snow on the ice and dissolved oxygen response, in a shallow eutrophic lake. The steady decline of oxygen during the long period of snow cover in 1939-40 (Fig. 14) contrasts strongly with the almost level (and relatively high) curve for the winter of 1937-38, a winter of comparatively little snowfall. A similar contrast exists between the curves for the two years 1940-41 and 1942-43 (Fig. 15).

The typically dystrophic water of Bog Lake shows, in comparison with the water of the other lakes studied, a set of extremes. In some cases its extreme stratification was almost unbelievable. For example, on January 23, 1941, the oxygen at the surface was 20.2 p.p.m., while at the depth of 5 feet it was 0.0 p.p.m. Most of this difference of 20.2 p.p.m., 16.2 p.p.m. to be exact, occurred between the one-foot level (18.3 p.p.m.) and the two-foot level (2.1 p.p.m.). No doubt such sharp stratification is associated with the brown suspended material of this bog water, and could very seldom if ever be found in a clear-water lake. Also greatly marked is the response of the surface water of Bog Lake (and to a certain extent the water at 1 and 2 feet) to changes in light conditions. This is quite evident in the fluctuations of the oxygen curves for 1939-40 (Fig. 16) in respect to the corresponding changes in the snow-depth curve.

As will be discussed below, under Experimental Studies, it is probable that the data from no one station in Pasinski's Pond can give a very complete

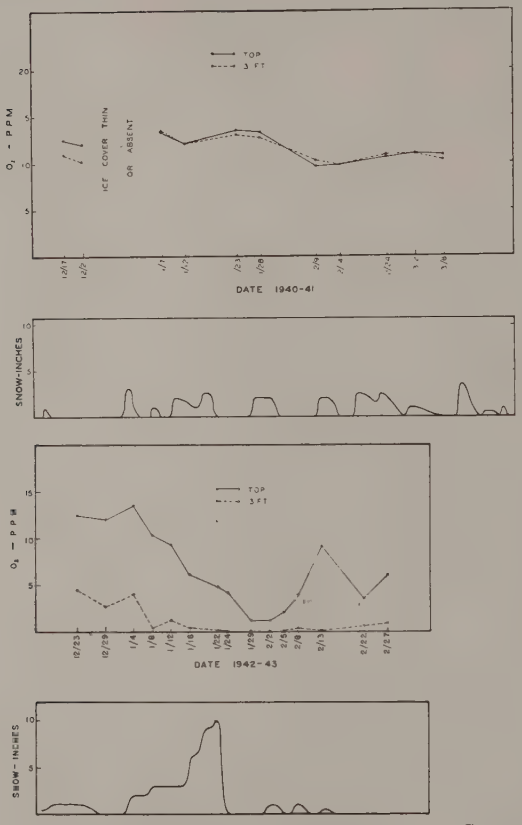

FIG. 15. Dissolved oxygen and snow cover, Green Lake, Station 1, 1940-41 and 1942-43.

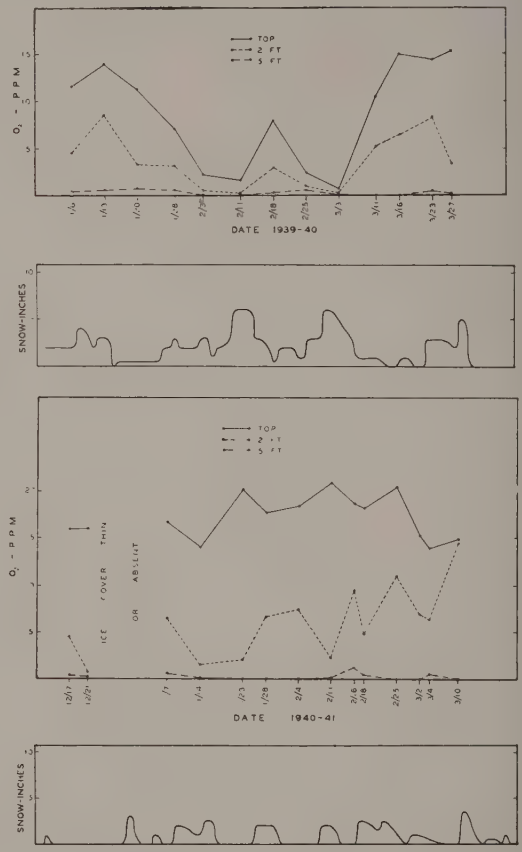

FIG. 16. Dissolved oxygen and snow cover, Bog Lake, 1939-40 and 1940-41.

picture of conditions in the pond as a whole, since the pond varies so greatly from one part to another. Especially does this qualification pertain to the winter 1939-40. In 1940-41 conditions were somewhat more nearly uniform throughout the pond, and hence may be studied with a fair degree of reliability by the use of one set of curves. Figure 17 gives the oxygen values for Station 26, the deepest station in the pond, for 1940-41. Here it may be noted that, as in the case of other lakes, there is a considerable correspondence in the dissolved oxygen values for the various depths on the same dates. In this instance, however, there are certain deviations from that coordination. The value for the bottom water fluctuated to some extent without respect to that of the surface water, particularly on January 31, when the oxygen at the bottom fell off, while the upper water was gaining oxygen. The extremely high oxygen values at this station throughout most of the winter 1940-41 are indicative of abundant photosynthetic production of oxygen, during a winter of little snow.

The variations in the dissolved oxygen content from one winter to another within the same lake are shown in Figures 18 and 19. The oxygen in the water in

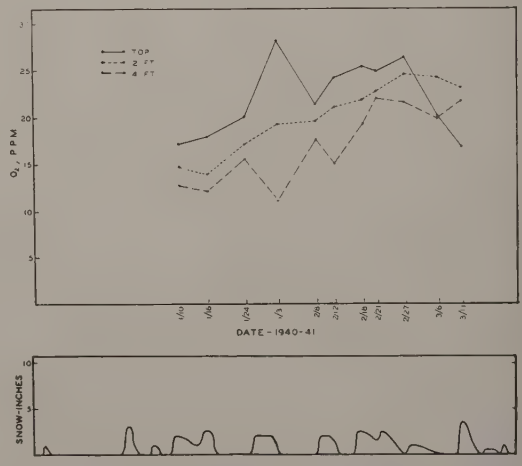

FIG. 17. Dissolved oxygen and snow cover, Pasinski's Pond, Station 26 (south end of pond), 1940-41.

Clear Lake (at the surface) was almost the same in each of three winters, not deviating far from the saturation point most of the time. The evident conclusion is that this water, being only mildly eutrophic, contained not only very little dead organic matter to consume its oxygen, but also very little living phytoplankton to produce oxygen. Hence it simply retained its initial supply of oxygen throughout the winter, with little addition or loss. It became neither excessively low in oxygen during a winter of much snow (1939-40) nor excessively high in oxygen during a winter of little snow (1940-41). Such water probably would be safe from complete oxygen depletion in the longest, most severe winter of the past or future few centuries.

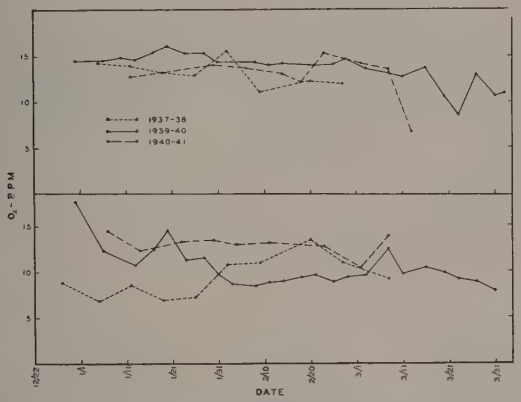

FIG. 18. Dissolved oxygen, different winters compared. Upper, Clear Lake, Station 1, surface. Lower, Mud Lake, Station 1, surface.

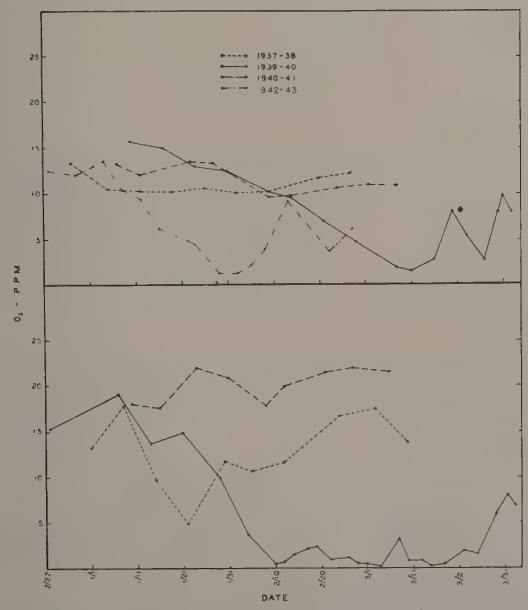

FIG. 19. Dissolved oxygen, different winters compared. Upper, Green Lake, Station 1, surface. Lower, Pasinski's Pond, Station 15 (north end of pond), surface.

The curves for Mud Lake and Green Lake (especially the latter), however, very plainly show the comparative effects of the different winters on the dissolved oxygen content of the water. The winter of 1939-40 had the most adverse effect, that of 1940-41 the least. The dissolved oxygen in Green Lake diminished rapidly in the early part of the winter of 1942-43, but rose rapidly following the disappearance of the snow cover. The greatest difference, in the examples chosen, is furnished by the curves for Pasinski's Pond, which form an almost perfect spread according to the severity of the different winters.

The vertical distribution of dissolved oxygen for various lakes and for certain selected dates is shown in Figures 20 to 22. In each of these figures the horizontal scale (oxygen) is the same throughout the figure. The vertical scale (depth) varies, in Figure 20, with the lake. This method of diagramming dissolved oxygen is similar to that sometimes used to show the vertical distribution of plankton. Included in Figure 20, for purposes of comparison, are diagrams for Lake Mendota, for certain dates in the winter of 1906-07, the data for which were taken from Birge & Juday (1911).

Changes in vertical distribution of oxygen take place as the winter season progresses. For instance, as mentioned above, the water of Clear Lake was almost uniform, as regards dissolved oxygen content, at all depths at the start of the ice cover in 1939-40. Oxygen at the lower depths gradually decreased, until on March 16 it was very much less than at the surface (correspondingly, the diagram for that date is semi-triangular). A somewhat similar sequence is shown by the diagrams for Lake Mendota, on the same figure, except that the oxygen in Lake Mendota tended to decrease mainly at the bottom, maintaining a somewhat uniform distribution in the upper half of the water. Lake Mendota of course is much deeper than Clear Lake.

However, in Clear Lake in 1940-41, as well as in Green Lake in the same winter, stratification was fairly well developed early in the winter, and the general shape of the oxygen distribution diagram remained somewhat the same throughout the winter. Some rather bizarre figures appear in Figure 20, most of which are occasioned by the somewhat sharp changes in the oxygen of the surface water, such as in Clear Lake on March 13, 1941, when run-in water had appreciably lowered the oxygen in the surface water.

The diagrams for Green Lake, 1942-43 (Fig. 21) depict a steady decrease in dissolved oxygen, first in the bottom water and then at the surface, throughout the early winter. This was followed by pronounced recovery, in the upper water, in the latter half of February.

In Bog Lake, in each of two winters, the oxygen at the bottom was very low even at the start of the

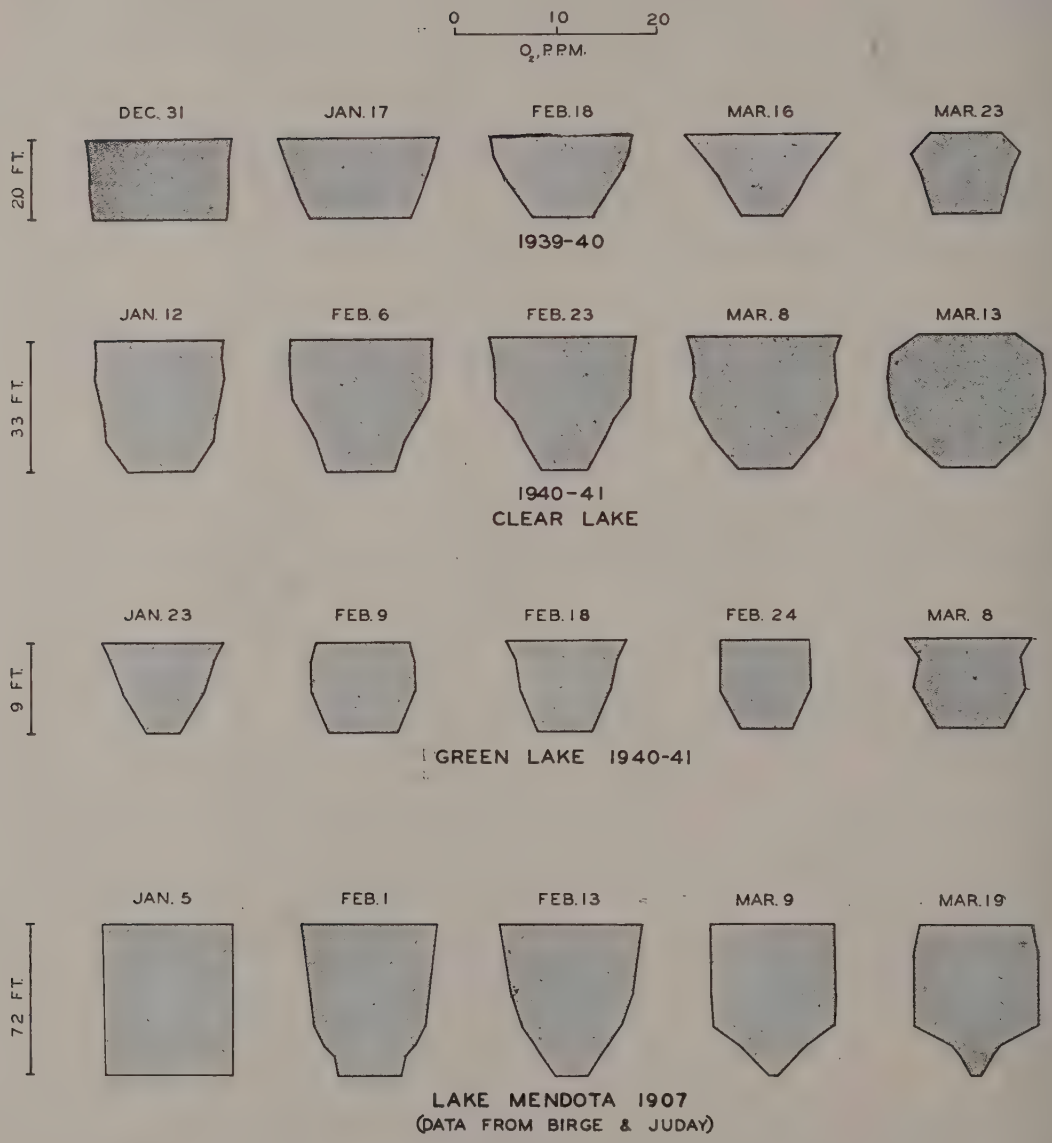

FIG. 20. Dissolved oxygen, vertical distribution. Clear Lake, Green Lake, and Lake Mendota, selected dates. The width of the block diagram at any given depth indicates the amount of oxygen present at that depth.

winter. Here, however, rapid and extreme changes occurred in the amount of oxygen in the upper water, so that the diagrams of Figure 22 vary exceedingly, from the almost perfect triangle for January 30, 1940, to the thin wedge for March 3 of the same winter, to the wine-glass shaped figure for December 21, 1940.

The peak values of dissolved oxygen mentioned above (i.e., 21.0 p.p.m. for Bog Lake and 28.0 p.p.m. for Pasinski's Pond, in 1940-41) are somewhat unusual for ice-covered water, although the literature has recorded a few similar instances. Griffiths (1936) reported an oxygen content of 22.0 p.p.m. for Long Pool, England, under the ice in February, 1930. In Lake Mendota (Birge & Juday 1911) on March 29, 1906, the upper water contained 12.5 cc. per liter (equal to about 17.0 p.p.m.) of oxygen. Knauthe (1899) reported the astoundingly high figure of 49.0 cc. per liter (about 70.0 p.p.m.) in an ice-covered pond which contained very large numbers of algae. There is considerable doubt, however, that his method of dissolved oxygen determination was a reliable one.

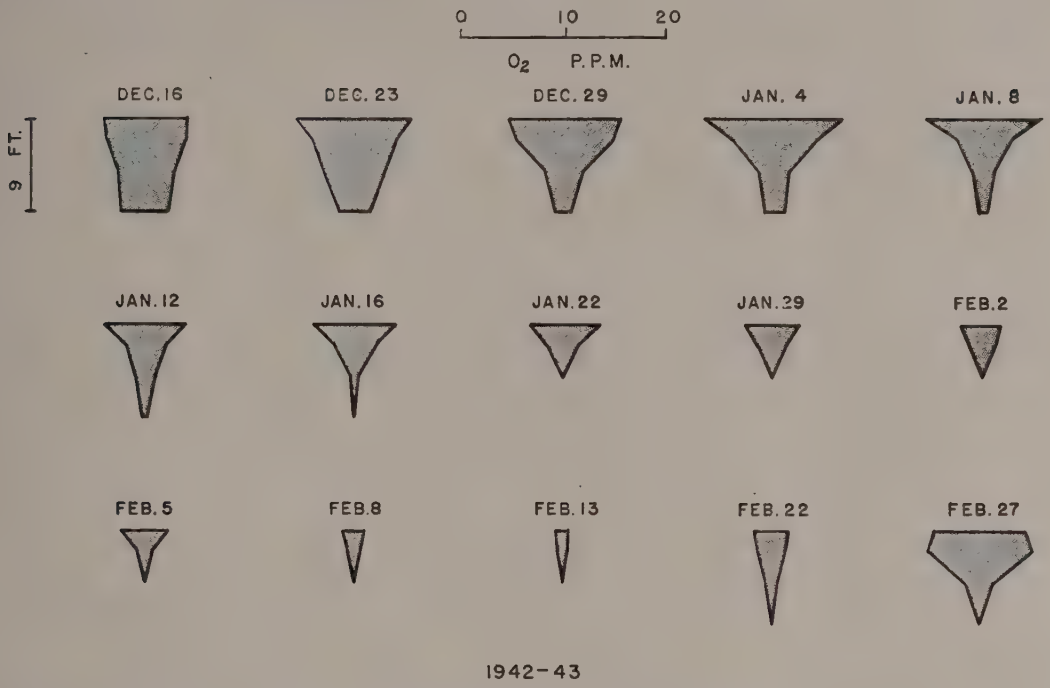

FIG. 21. Dissolved oxygen, vertical distribution. Green Lake, selected dates, 1942-43. The width of the block diagram at any given depth indicates the amount of oxygen present at that depth.

SPECIAL OBSERVATIONS, GREEN LAKE

FORTY-EIGHT-HOUR OXYGEN VARIATIONS

In order to determine the effects of alternating light and dark periods upon the dissolved oxygen content of the water under the ice, and the possible existence of a diurnal oxygen cycle, a two-day run of sampling was conducted on Green Lake, from January 17 to 19, 1941. Samples were taken at two-hour intervals, starting at 5 P.M. on January 17, and ending at 3 P.M. on January 19.

The oxygen in the surface water remained practically constant throughout the forty-eight hours, the entire range of variation being between 12.3 and 14.3 p.p.m. The slight fluctuations showed no apparent correlation with periods of light and dark.

Much greater changes appeared in the values for the deeper samples. The variation at 5 feet was from a low of 7.2 to a high of 10.5 p.p.m., and 9 feet from 3.4 to 7.6 p.p.m. Again no correlation with daylight and dark was evident.

The situation of greater fluctuation in the deeper water than at the surface is exactly the reverse of that which would be expected if changes in light were the cause of fluctuation, since the upper water is more subject to these changes. The fluctuations in the values for the lower depths were apparently quite at random, and probably are largely explainable by imperfections in the sampling technique (i.e., inability in sampling to strike exactly the same depth each time), or by shifts in the stratified layers of water.

No well-defined, if indeed any, diurnal variation in oxygen was present. Perhaps this is due to the fact that the processes of photosynthesis and decomposition are considerably slowed down at low temperatures, and hence do not reflect the diurnal changes in light.

This example of course does not prove that diurnal variations in dissolved oxygen under the ice never exist. It may be that at certain times, particularly during periods of unusually high oxygen production (as in Pasinski's Pond in 1940-41), a slight diurnal cycle is present. However, for the average ice-bound lake, it is probable that diurnal variations in oxygen are insignificant.

DISSOLVED OXYGEN, TEMPERATURE, AND ALKALINITY PROFILES

Profile sections of Green Lake, showing isograms of dissolved oxygen, were drawn up for one date in 1940-41 and three dates in 1942-43. Briefly, these profiles were derived as follows. Oxygen determinations were made, at depth intervals of one foot, and at a series of stations at regular horizontal intervals along a line from the mouth of the inlet stream to the dam. This line made a broad curve, roughly following the channel of current, and including Stations 4, 2, 1, and 5 (see Figure 5). The diagrams (Figs. 23-25) are drawn in idealized profile plan, with isograms connecting points of equal dissolved oxygen.

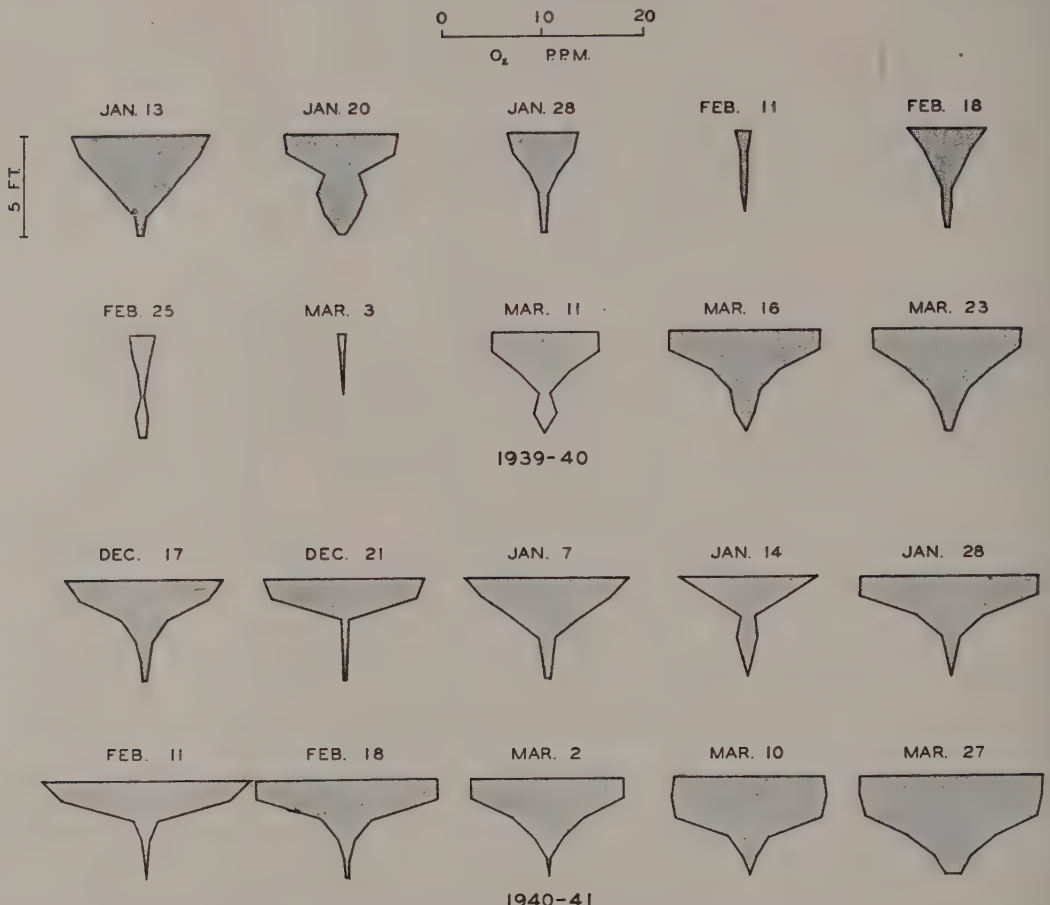

FIG. 22. Dissolved oxygen, vertical distribution. Bog Lake, selected dates, 1939-40 and 1940-41. The width of the block diagram at any given depth indicates the amount of oxygen present at that depth.

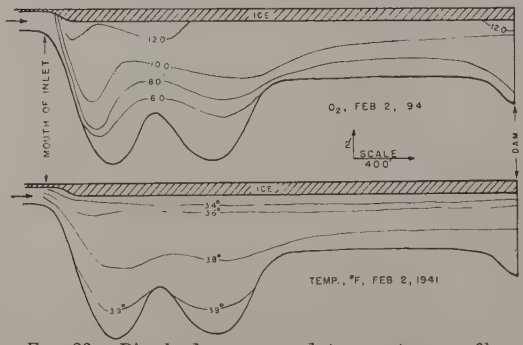

FIG. 23. Dissolved oxygen and temperature profiles, Green Lake, February 2, 1941. See text for description.

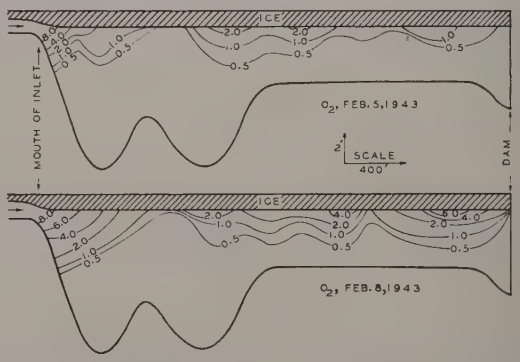

FIG. 24. Dissolved oxygen profiles, Green Lake. Upper, February 5, 1943. Lower, February 8, 1943. See text for description.

The vertical scale is greatly exaggerated with reference to the horizontal scale.

A similar diagram showing isothermal lines, and another with isograms of methyl orange alkalinity (each for one date only) were constructed (Figs. 23 and 25).

As shown by the diagrams, the dissolved stratification is sharpest near the bottom, and the oxygen isograms tend to follow the bottom contour. On the other hand, the temperature changes most rapidly

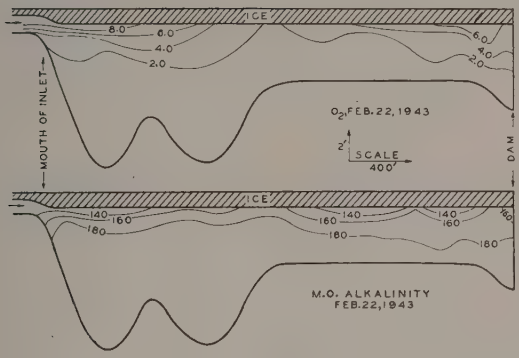

FIG. 25. Dissolved oxygen and methyl orange alkalinity profiles, Green Lake, February 22, 1943. See text for description.

immediately under the ice, and the isotherms tend to be parallel to the surface contour.

The profile of February 2, 1941, represents the lake at a time of relatively high dissolved oxygen; those of the three dates in 1943 show comparatively low oxygen. On February 5, 1943, only a small part of the area of the transect had an oxygen value of 2.0 p.p.m. or more, and by far the largest part had less than 0.5 p.p.m. The inflowing water, however, was carrying over 8 p.p.m. at this time. The amount of oxygen enrichment which thus far had been brought about by this means is evident from the diagram. It must be remembered, of course, that the diagram represents a section along the channel; the effect of the inlet upon the lake as a whole is not nearly so great.

The oxygen along the profile had increased noticeably by February 8, chiefly as a result of rains and thaws. That this increase came from the surface is well indicated in the diagram, which shows a vertical shift in the isograms. However, in spite of this shift, the same general pattern was carried over from the one date to the other. During the three-day interval a large amount of water, relatively high in oxygen, was brought in by the inlet stream; its effect is displayed in the changed pattern of the isograms at that end of the section.

By February 22, a considerable amount of oxygen had been added to the upper water, by inflowing water (possibly also to some extent by photosynthesis), almost completely obliterating the former pattern of the profile. A few vestiges of that pattern remained, however, particularly the "low" point at about 1,500 feet from the mouth of the inlet. The local effect of water from the inlet stream had largely been absorbed by, even as it contributed to, the general increase in oxygen in the upper layers of water.

Evidence that much of the change was caused by inflowing water is given by the diagram for methyl orange alkalinity, for the same date (February 22). The alkalinity isograms tended somewhat to follow those for oxygen. The normal situation toward the end of winter stagnation is for the alkalinity to be greatest at the bottom, and least just under the ice. But without the entrance of relatively soft water (from surface or other inflow), the alkalinity at the surface in Green Lake usually does not fall below 175 p.p.m. The values, shown on the diagram, of 140 p.p.m. or less, definitely are attributable to inflowing water.

An index, by means of which the relative average amounts of oxygen represented on the four dissolved oxygen profile diagrams may be compared, has been derived as follows. For each diagram, the area between each two consecutive isograms was measured, and computed in terms of percent of the total area of the diagram. This figure then was multiplied by the mean oxygen value of the two isograms. These products were totalled, and their sum divided by the total area (i.e., by 100 percent). The quotient was assumed to represent the average value for the entire diagram, and thus for that transverse section of the lake at the time.

How reliably this index may be applied to the lake as a whole is not known, for of course only one section is represented, and that a rather special one (along the channel). However, it surely is a much better index that one obtained from only a single station; and it at least gives a general idea of the condition of the entire lake.

These calculated mean values were:

Feb. 2, 1941	9.3 p.p.m.
Feb. 5, 1943	0.6 p.p.m.
Feb. 8, 1943	1.0 p.p.m.
Feb. 22, 1943	2.1 p.p.m.

These figures show something of the increase (mentioned above) of oxygen during February, 1943. They also point out that which is not instantly apparent in the diagrams, that is, that as concerns the section as a whole the increase in oxygen was not numerically great, even though the water near the surface did become much enriched in oxygen. A lake may show apparently great recovery from low oxygen conditions, when judged by one or a few surface samples, and yet continue to be relatively low in average oxygen content. In fact, it often is the case, in the average eutrophic lake in this region, that the oxygen near the bottom diminishes quickly after the lake becomes ice-covered, and remains low throughout the winter; thus the shifting back and forth between high and low oxygen values occurs only in the water near the surface. In effect, a "squeezing-out" is accomplished; that is, the fish presumably are confined, for a large part of the winter, to a more or less thin layer of water immediately under the ice.

pH, Carbon Dioxide, Alkalinity

A fairly complete set of observations were made of pH, methyl orange alkalinity, and (particularly in 1940-41) free carbon dioxide. These figures are not presented here in tabular form, since they are largely repetitious.

Except for the occasional influence of melted snow or ice, or rain, on surface samples, the pH in any particular lake tended to change little throughout a winter. All of the lakes studied, except Bog Lake, had water of comparatively high buffering capacity, and the pH usually remained reasonably close to the figure pH 8.0, dropping below 7.0 only at times of serious decomposition.

Even the water of Bog Lake, with its extremely low bicarbonate content, showed a fluctuation, around the value pH 6.0, of only about 1.0 pH unit.

Likewise, significantly large quantities of titratable ("free") CO_2 were seldom found. Even at times of oxygen depletion, the hard-water lakes showed only a few p.p.m. of free carbon dioxide. Bog Lake, with its soft, acid water, always contained titratable acidity (probably caused by other acids in conjunction with carbonic acid), but usually in amounts of less than 30 p.p.m.

In general, the condition of the water, as regards the welfare of aquatic organisms in the winter, is described more forcefully and understandably by dissolved oxygen data and graphs than by the figures for alkalinity and CO_2. A few general observations regarding the alkalinity values are in order, however.

As might be expected, free CO_2 and pH are fairly closely correlated with dissolved oxygen. The same processes of decay which use oxygen produce carbon dioxide, and hence lower the pH. Conversely, the photosynthetic production of oxygen uses up carbon dioxide and raises the pH. To a certain degree, therefore, CO_2 or pH could furnish a rough index to conditions under the ice, especially if the usual or normal values were known. However, certain complications, some of which are unforeseen, may arise.

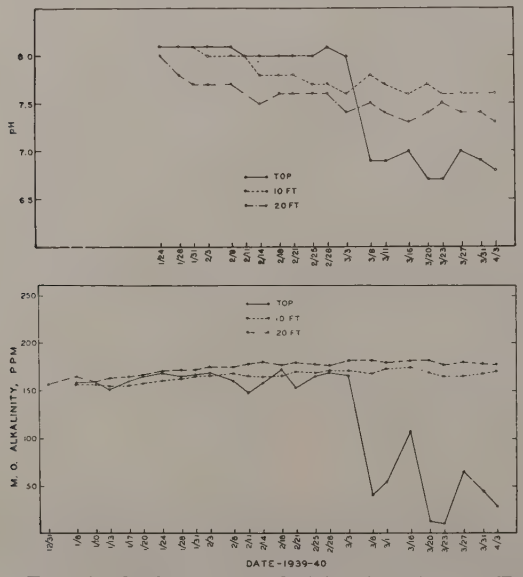

FIG. 26. Methyl orange alkalinity (lower) and pH (upper). Clear Lake, Station 2, 1939-40.

The pH sometimes is influenced (in bog lakes especially) by acids other than carbon dioxide. Inflowing water, from melted snow and ice, may greatly alter (lower) the buffering power of the water, and hence affect pH (see Figure 26).

The physiological significance of free carbon dioxide is discussed briefly below in the section on winter suffocation.

Under the influence of developing stagnation, the so-called total alkalinity, or alkalinity to methyl orange, gradually increases by a relatively small amount. With conditions of stratification, the water near the bottom usually has a higher methyl orange alkalinity than that near the surface. Figure 26 (for Clear Lake, 1939-40) shows this difference, as well as the tendency for the curves representing the alkalinity at various depths to spread apart as the winter progresses, after starting at almost the same value. This behaviour is somewhat comparable to that of the dissolved oxygen curves for the same station. The sharp fluctuations and extremely low alkalinity values shown by the curve of the surface were caused by dilution with rain or melted snow or ice.

BIOCHEMICAL OXYGEN DEMAND

The biochemical oxygen demand (abbreviated B.O.D.) is the oxygen consumed, by bacterial action,[2] in a certain period of time, from a sample incubated in the dark at a fixed temperature. Conventionally, if the limiting conditions are not indicated, it is understood that the time period is five days (120 hours) and the incubation temperature 20° C. In the present series of B.O.D. determinations a considerable number of samples were incubated at 0° C., and some of these had an extended incubation up to 60 days.

B.O.D. gives a rather accurate picture of the relative organic richness of a water sample, and the likelihood of the depletion of its dissolved oxygen supply in a given time. When measured at 0° C., the B.O.D. of a sample of water from an ice-covered lake provides a rough indication of the probable behaviour of that water with respect to oxygen depletion.

The B.O.D. data obtained are summarized in Tables 3-5. As mentioned above, in the section on Methods, the values given in these tables usually are weighted means of two or more samples, set up at different dilutions. Table 3 gives the B.O.D. values for five-day incubation at 20°, and Table 4 those for five days at 0°. Table 5 is for the 60-day B.O.D. run at 0°.

Certain facts are apparent. The B.O.D. of the water in Clear Lake was very much less than that of the more eutrophic waters. Extremely high B.O.D. was found for many samples from Bog Lake and Pasinski's Pond. The B.O.D. at 0° C., for nearly all of the waters studied, showed a correlation with that at 20°. The values for 0° averaged on the order of four-tenths of those for 20°.

[2] Theoretically only bacterial action (and possibly that of algae, protozoa, and microscopic metazoa) is involved. Actually a part of the demand (usually a small part) may come from purely chemical oxidation.

TABLE 3. Biochemical oxygen demand (B.O.D.), five days at 20° C. Samples from various lakes, 1940-41. Data expressed in p.p.m.

Lake	Station number	Depth	Dates								
			12/21	1/7	1/23	1/28	2/9	2/18	3/11		
Green	1	Surface	2.9	2.0	....	3.0	2.3	.....	..		
		Bottom	1.7	2.4	....	2.3	1.8	.....	..		
	2	Surface	1.5	1.9	1.9	3.8	1.5	2.0	....		
		2 feet	.....	.....	1.6	2.0	2.1	.....	2.0		
		5 feet	2.0	2.6	0.3	2.6	2.1	2 2	....		
		9 feet	0.0	1.9	3.0	1.9	1.1	2.1	...		
	3	Surface	3.2	3.1	....	3.3	2.4	.....	....		
		Bottom	2.7	2.9	....	3.9	3.2	.....	....		
	4	Surface	2.9	1.8	..	2.8	3.3	.....	....		
		4 feet	.....	.....	....	2.2	.....	.....	....		
		8 feet	2.3	0.8	....	0.0	3.1	.....	....		
	5	Surface	.....	3.1	....	2.6	1.4	.....	....		
		Bottom	.....	2.9	....	2.9	1.8	.....	....		
	Inlet		2.0	0.0	1.5	0.8	1.0	.....	....		
	Outlet		1.7	4.0	....	2.7	2.5	.....	....		
			12/19	1/7	1/14	1/23	1/30	2/4	2/11		
Mud	1	Surface	2.1	3.1	1.4	2.6	3.7	2.6	3.9		
		Bottom	1.3	2.2	1.4	1.9	2.2	2.1	2.4		
	Inlet		2.1	2.1	2.7	2.0	2.2	1.5	1.3		
	Outlet		2.1	2.1	2.6	2.3	4.3	2.4	2.6		
			12/21	1/12	1/23	1/30	2/6	2/18	3/11		
Clear	1	Surface	.....	1.2	....	3.8	2.9	1.6	....		
		Bottom	.....	0.5	1.8	1.7	2.1	.....	1.2		
	2a	Surface	2.3	0.8	2.2	4.3	3.2	.....	....		
		5 feet	.....	0.6	1.5	2.4	1.8	.....	....		
		10 feet	1.5	0.8	1.6	3.6	2.3	.....	....		
		15 feet	.....	0.6	1.7	1.8	1.0	.....	....		
		20 feet	1.6	0.0	2.8	1.2	1.9	.....	....		
		25 feet	.....	0.0	1.4	0.9	1.3	.....	....		
		33 feet	0.0	0.0	0.0	0.0	0.0	.....	....		
			12/21	1/7	1/14	1/23	2/4	2/11	2/18	3/11	
Bog		Surface	13.4	15.2	9.8	10.0	13.2	8.8	12.0	22.0+	
		1 foot	8.4	8.2	5.2	18.3	7.3	8.4	.....	.....	
		2 feet	1.4	5.6	2.2	5.1	7.0+	2.0+	4.2	7.2	
		3 feet	1.8	1.8	4.0	3.9	5.6	3.0	.....	.....	
		4 feet	2.2	3.6	2.8	4.6	3.8	3.8	.....	.....	
		5 feet	2.2	2.6	3.4	4.2	4.2	3.4	6.2	2.9	
			12/19	1/10	1/16	1/24	1/31	2/8	2/12	2/18	3/11
Pasinski's Pond	15	Surface	3.0	15.0	42.0	10.6	14.7	6.8	12.0	.....	.....
		Bottom	1.3	2.5	5.7	11.2	2.6	5.7	2.7	.....	.....
	24	Surface	.....	7.6	6.2	5.2	10.0	11.0	20.2	.....	.....
		Bottom	.....	1.1	5.5	4.8	4.0	5.9	7.9	.....	.....
	26	Surface	4.2	11.5	11.0	2.8	8.3	2.5	36.3	6.4	22.0+
		1 foot	.....	4.4	4.5	2.4	9.2	9.4	34.3	.....	.....
		2 feet	.....	4.2	3.1	6.1	5.3	7.6	20.1	10.0	8.4
		3 feet	.....	4.0	2.8	5.8	2.6	11.0	15.7	.....	.....
		4 feet	1.5	1.7	4.9	4.4	1.4	10.9	6.1	7.5	5.4
	27	Surface	.....	12.9	7.1	4.3	21.8	4.8	24.2	.....	.....
		Bottom	.....	4.7	0.0	3.6	5.2	6.3	3.6	.....	.....
	20	Surface	.....	6.7	9.1	10.1	10.0	8.1	20.6	.....	.....
		Bottom	.....	3.2	0.0	4.8	3.6	5.2	3.2	.....	.....

TABLE 4. Biochemical oxygen demand (B.O.D.), five days at 0° C. Samples from various lakes, 1941. Data expressed in p.p.m.

Lake	Station number	Depth	Dates			
			2/9	2/18	3/11	
Green	1	Surface	0.6	..	.	
		Bottom	0.8	...	...	
	2	Surface	0.7	0.0	...	
		2 feet	1.3	...	0.5	
		5 feet	0.8	0.3	..	
		9 feet	0.0	0.4	...	
	3	Surface	1.2	...	...	
		Bottom	1.8	...	...	
	4	Surface	0.6	...	...	
		Bottom	3.3	...	...	
	5	Surface	0.5	...	...	
		Bottom	0.6	...	...	
	Inlet	.....	0.6	...	...	
	Outlet	.....	0.9	...	...	
			2/4	2/11		
Mud	1	Surface	0.5	1.2		
		Bottom	0.6	1.4		
	Inlet	.....	0.0	0.6		
	Outlet	.....	1.0	1.3		
			2/6	2/18	3/11	
Clear	1	Surface	0.0	0.0	...	
		Bottom	0.5	...	0.0	
	2a	Surface	0.0	...	...	
		5 feet	0.4	...	...	
		10 feet	0.4	...	...	
		15 feet	0.0	...	...	
		20 feet	0.3	...	...	
		25 feet	0.7	...	...	
		33 feet	0.0	...	...	
			2/4	2/11	2/18	3/11
Bog	.....	Surface	3.9	4.1	2.4	9.4
		1 foot	1.1	6.1	...	...
		2 feet	5.4	1.4	1.2	2.8
		3 feet	0.0	0.0	...	...
		4 feet	0.0	0.0	...	...
		5 feet	0.0	0.0	1.0	1.4
			2/8	2/12	2/18	3/11
Pasinski's Pond	15	Surface	1.1	5.7	...	...
		Bottom	3.0	1.9	...	...
	20	Surface	2.7	7.8	...	...
		Bottom	2.8	0.5	...	...
	24	Surface	3.4	9.4	...	...
		Bottom	3.9	8.4	...	...
	26	Surface	0.0	16.1	1.1	22.7
		1 foot	0.0	15.3	...	...
		2 feet	3.0	7.5	2.8	4.0
		3 feet	2.8	5.8	...	...
		4 feet	2.5	2.9	2.5	2.2
	27	Surface	4.1	11.8	...	...
		Bottom	4.1	1.9	...	...

Worthy of note is the regularity with which the B.O.D. at any particular station was higher in the upper water than near the bottom. Sometimes the differences were very large, such as that between 24.2 p.p.m. and 3.6 p.p.m., at Pasinski's Pond, Station 27, February 12, 1941. This sharp decline of B.O.D. with increasing depth probably indicates a greater accumulation of suspended organic materials, such as zooplankton and phytoplankton, in the surface waters. Given the right conditions of darkness, and so forth, as in a B.O.D. sample bottle, this material decomposes rather rapidly, giving a high B.O.D. figure.

TABLE 5. Biochemical oxygen demand (B.O.D.), 60 days at 0° C. Samples taken March 11, 1941. Data expressed in p.p.m.

Lake	Station	Depth	Days	B.O.D., p.p.m.	Lake	Station	Depth	Days	B.O.D., p.p.m.
Clear	1	3 feet	5	0.0	Green	2	3 feet	5	0.5
			10	1.6				10	1.7
			15	2.1				15	1.8
			20	1.3				20	1.8
			30	0.2				30	2.2
			40	2.8				40	7.0
			50	1.9				50	5.4
			60	2.6				60	5.4
Bog		Sur-	5	9.4	Pasinski's	26	Sur-	5	22.5
		face	10	20.0	Pond		face	10	29.6
			15	27.6					
			20	31.6			2 feet	5	4.0
								10	4.0
		2 feet	5	2.8				15	7.4
			10	4.9				20	9.5
			15	5.4				20	14.6
			20	6.5				30	15.2
			30	8.3				40	18.4
			40	9.5				50	18.0
			40	15.4					
			50	....			4 feet	5	2.2
			60	20.4				10	4.3
								15	5.2
		5 feet	5	1.4				20	5.0
			10	4.4				30	6.9
			15	5.2				40	6.7
			20	5.8				50	6.7
			30	8.8				50	11.6
			40	10.8					
			50	7.6					

In the water under the ice, this suspended organic matter settles slowly, probably being oxidized as it sinks. Hence its power of utilizing oxygen is diminished by the time it reaches the lower water.

Opposed to this reasoning stands the fact that the upper water usually maintains, throughout the winter, much more oxygen than does the bottom water. This difference, however, can at least in part be accounted for by the much greater production of oxygen in the upper water.

The high B.O.D. values obtained for certain samples (Tables 3 and 4) indicate water exceedingly rich in organic material. Many samples from Pasinski's Pond had a 5-day demand, at 20°, of over 25 p.p.m., with a high of 42.0 p.p.m. These values are even higher than those of some badly polluted waters. For instance, in the waters of Green Bay (Williamson et al. 1939), which were subject to sulfite pulp mill pollution, most of the samples taken had a 5-day B.O.D. of 10 p.p.m. or less; and even in the extremely putrid waters of East River values higher than 25 p.p.m. were very seldom encountered.

Figure 27 shows the B.O.D. at 0° C., over an extended period of time, of three samples from Station 26, Pasinski's Pond, and one sample from Clear Lake (the samples were taken on March 11, 1941). The curves as drawn are somewhat idealized, because too few data are at hand to make sure the exact shape of the curves. However, they are of the same shape as B.O.D. curves in general.

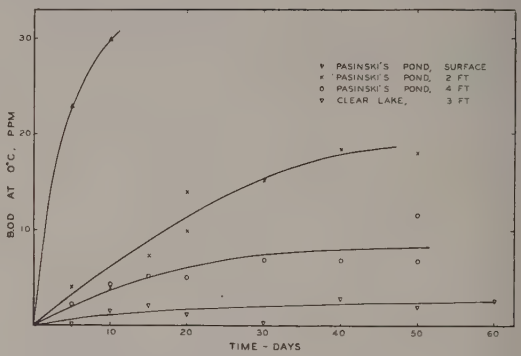

FIG. 27. Biochemical oxygen demand at 0° C. Samples taken March 11, 1941.

The curves for the three depths in Pasinski's Pond exhibit a remarkable spread, and also quite a contrast to the almost flat curve for Clear Lake. The water at the surface in Pasinski's Pond had approximately nine times as much B.O.D. in five days (22.5 p.p.m.) as did that in Clear Lake in sixty days (2.6 p.p.m.). Such comparative figures go far toward explaining why Pasinski's Pond can lose nearly all of its dissolved oxygen within a few days, while Clear Lake almost invariably retains oxygen nearly to the saturation point throughout the entire winter.

LIGHT PENETRATION

During the winters of 1940-41 and 1942-43, a considerable number of measurements were made of the transmission of light through water, ice, and snow, in the various situations which obtained at the lakes which were being investigated. The photometer used, and the methods employed, are described above. In order to utilize deeper snow than was available on the lakes in the Ann Arbor region, visits were made to certain lakes in Iosco and Montmorency counties, Michigan. The light transmission data are summarized in Tables 6-9.

Considerable information may be obtained from the literature. Numerous papers have been written concerning light penetration into water, both sea water and that of lakes. Among the many investigators who have done work on this subject, there may be mentioned Clarke, Shelford, Poole & Atkins, Utterback, Birge & Juday, and Pearsall & Ullyott, most of whom are cited below. Although much less work has been done on snow and ice, a few informative papers have appeared.

TRANSMISSION THROUGH WATER

The characteristics of various waters with respect to the transmission of light have been reviewed by Welch (1935, pp. 72-79), Birge & Juday (1929), and more recently by Clarke (1939) and by Utterback (1941), and therefore are only briefly mentioned here. The observations of this study agree, in general, with the conclusions of these various writers.

It is well known that even the clearest waters impede the passage of light to a certain extent. Light

TABLE 6. Light transmission through water, ice, and snow. Field measurements at certain lakes, 1941. Results expressed in foot-candles incident on photometer target, and in percentage transmission.

Date, 1941	Ice		Snow		Depth[1]	Intensity, foot-candles	Percentage Transmission			
	Thickness, inches	Condition	Thickness, inches	Condition			No filter	Red	Green	Blue
CLEAR LAKE										
Feb. 23	7½	Clear	None	.....	Air	8000	.....	.....	.....	.....
					Ice	6700	84	.....	.....	.....
					1′	5400	68	.....	.....	.....
					2′	4560	57	.....	.....	.....
					3′	3800	48	.....	.....	.....
					6′	1920	24	.....	.....	.....
					9′	1360	17	.....	.....	.....
					12′	820	10.2	.....	.....	.....
					15′	580	7.2	.....	.....	.....
					18′	400	5.0	.....	.....	.....
					21′	300	3.8	.....	.....	.....
					24′	206	2.6	.....	.....	.....
					27′	142	1.8	.....	.....	.....
					30′	112	1.4	.....	.....	.....
	7	Clear	7/8–1	Dry, light	Air	7300	.....	.....	.....	.....
					Ice	182	2.5	.....	.....	.....
	(Same)		(Snow removed)		Air	7000	.....	.....	.....	.....
					Ice	3800	54	.....	.....	.....
Mar. 13	6	—	None	.....	Air	4800	.....	.....	.....	.....
					Ice	2540	53	53	53	54
					3′	1400	29	27	32	28
					6′	1000	21	16	23	13
					9′	690	14.4	9.8	16	7.4
					12′	490	10.2	6.0	12	4.0
					15′	340	7.1	4.0	8.7	2.4
					18′	250	5.2	2.6	6.6	1.5
					21′	188	3.9	1.7	5.0	0.9
					24′	138	2.9	1.2	3.7	0.5
					27′	100	2.1	0.8	2.8	0.3
					30′	76	1.6	0.5	2.2	0.2
					32′	55	1.1	0.4	1.6	0.2
GREEN LAKE										
Mar. 13	5	Fairly clear	None	.....	Air	2120	.....	.....	.....	.....
					Ice	1250	59	57	59	58
MUD LAKE										
Feb. 23	8½	Clear	None	.....	Air	3200	.....	.....	.....	.....
					Ice	2150	67	.....	.....	.....
	7½	Partly cloudy	None	.....	Air	3700	.....	.....	.....	.....
					Ice	820	22	.....	.....	.....
	10¾	Very cloudy	None	.....	Air	4700	.....	.....	.....	.....
					Ice	340	7.2	.....	.....	.....
	6½	Clear	2–2½	Crusted	Air	5550	.....	.....	.....	.....
					Ice	55	1.0	.....	.....	.....
	(Same)		(Snow removed)		Air	5900	.....	.....	.....	.....
					Ice	3100	53	.....	.....	.....
BOG LAKE										
Feb. 25	9½	Milky	1–7/8	Dry, light	Air	9200	.....	.....	.....	.....
					Ice	106	1.15	.....	.....	.....
	(Same)		(Snow removed)		Air	9300	.....	.....	.....	.....
					Ice	1340	14.4	.....	.....	.....
	9½	Milky	1⅞	Dry	Air	9440	.....	.....	.....	.....
					Ice	154	1.63	.....	.....	.....
					2′	100	1.06	.....	.....	.....
					3′	27	0.29	.....	.....	.....
					4′	12.4	0.13	.....	.....	.....
					5′	7.0	0.07	.....	.....	.....

TABLE 6 (continued)

Date, 1941	Ice		Snow		Depth[1]	Intensity, foot-candles	Percentage Transmission			
	Thickness, inches	Condition	Thickness, inches	Condition			No filter	Red	Green	Blue
Mar. 13	10	Soft on top	1	Slushy	Air	3450	.....	.....	.....	.....
					Ice	138	4.0	4.5	4.0	2.5
					13″	.....	.....	.....	.....	0.19
					15″	.....	.....	.....	.....	0.19
					24″	17	0.49	1.14	0.42	.....
	(Same)		(Snow removed)		Air	2500	.....	.....	.....	.....
					Ice	340	13.6	15.8	14.4	8.3
					13″	.....	.....	.....	.....	2.1
					16″	.....	.....	.....	.....	0.46
					24″	50	2.0	3.0	1.9	0.02
SOUTH LONDO LAKE										
Mar. 5	24	Partly cloudy	10	Dry	Air	7600	.....	.....	.....	.....
					Ice	4.0	0.05	.....	.....	.....
	(Same)		(Snow removed)		Air	7600	.....	.....	.....	.....
					Ice	580	7.6	.....	.....	.....
EAST FISH LAKE										
Mar. 20	14	Partly cloudy	5	Dry	Air	4650	.....	.....	.....	.....
					Ice	10.5	0.23	0.21	0.30	0.23
					3′	10.5	0.23	.....	.....	.....
					6′	9.0	0.19	0.13	0.24	0.15
					9′	7.2	0.15	0.09	0.18	0.09
					12′	5.5	0.12	0.07	0.14	0.07
					15′	4.5	0.10	0.05	0.11	0.06
					18′	3.8	0.08	0.04	0.10	0.04
					21′	3.2	0.07	0.03	0.07	0.04
					24′	2.7	0.06	0.03	0.06	0.03
					27′	2.2	0.05	0.02	0.05	0.03
					30′	1.6	0.03	0.02	0.04	0.02
	(Same)		(Snow removed)		Air	4950	.....	.....	.....	.....
					Ice	470	9.5	9.3	10.8	7.4
MIDDLE FISH LAKE										
Mar. 21	16	Fairly clear	6	Crusted	Air	9900	.....	.....	.....	.....
					Ice	9.3	0.09	0.10	0.11	0.05
					19″	8.5	0.09	0.10	0.11	0.05
					22″	7.8	0.08	0.09	0.10	0.04
					28″	7.2	0.07	0.09	0.10	0.03
	(Same)		(Snow removed)		Air	10600	.....	.....	.....	.....
					Ice	1220	11.5	11.3	12.2	8.1
					19″	1020	9.6	10.1	11.5	5.7
					22″	930	8.8	8.8	10.2	3.6
					28″	720	6.8	7.1	7.5	1.9
WEST FISH LAKE										
Mar. 21	16	Fairly clear	6½	Crusted	Air	10400	.....	.....	.....	.....
					Ice	9.4	0.09	0.07	0.13	0.12
					2′	8.7	0.08	0.07	.....	0.11
					3′	7.5	0.07	0.05	.....	0.06
					4′	6.8	0.07	0.05	.....	0.04
					5′	6.2	0.06	0.05	0.10	0.03
					6′	6.0	0.06	0.04	0.08	0.02
					7′	5.2	0.05	0.04	0.06	0.01
					8′	4.2	0.04	0.03	0.05	0.01

[1]Below upper surface of ice.

(in the yellow-green region of the spectrum) is reduced by passing through 100 meters of distilled water, to between 1 and 2 percent of its incident value (Clarke 1939). Natural waters vary from those almost as clear as distilled water, to the highly colored waters of bog lakes or the extremely turbid waters of silt-laden streams, in which the light may

TABLE 7. Light transmission through ice. Field measurements at certain lakes.

Lake	Date	Ice		Percentage Transmission			
		Thickness, inches	Condition	No filter	Red	Green	Blue
Clear	2/23/41	7½	Clear	84	....	....	....
Mud	2/23/41	8½	Clear	67	....	....	....
Green	3/13/41	5	Fairly clear	59	57	59	58
Clear	2/23/41	7	Clear	54	....	....	....
Mud	2/23/41	6½	Clear	53	....	....	....
Clear	3/13/41	6	Fairly clear	53	53	53	54
Mud	2/23/41	7½	Partly Cloudy	22	....	....	....
Bog	3/13/41	10	Soft on top	14	16	14	8.3
Bog	2/25/41	9½	Milky	14	....	....	....
Green	2/ 8/43	15	Cloudy on top	11.6	12.4	12.6	7.2
M. Fish	3/21/41	16	Fairly clear	11.5	11.3	12.2	8.1
E. Fish	3/20/41	14	Partly cloudy	9.5	9.3	10.8	7.4
Green	2/ 8/43	15	Cloudy on top	8.7	....	....	....
S. Londo	3/ 5/41	24	Partly cloudy	7.6	....	....	....
Mud	2/23/41	10¾	Very cloudy	7.2	....	....	....
Green	2/ 2/43	15	Cloudy on top	2.0	2.4	2.1	1.0

TABLE 8. Light transmission through snow. Field measurements at certain of the lakes studied. Percentage transmission obtained by calculation (see text).

Lake	Date	Snow		Percentage Transmission			
		Thickness, inches	Condition	No filter	Red	Green	Blue
Bog	3/13/41	1	Slushy	29	28	28	30
Green	2/ 2/43	1	Crusted	17	17	23	18
Green	2/ 8/43	1	Crusted	13	....	....	....
Green	2/ 8/43	1	Crusted	10.4	10.0	9.3	9.3
Bog	2/25/41	1⅞	Dry, light	8.0	....	....	....
Clear	2/23/41	7⅛ - 1	Dry, light	4.6	....	....	....
E. Fish	3/20/41	5	Dry	2.5	1.9	2.5	2.4
Mud	2/23/41	2 - 2½	Crusted	1.9	....	....	....
M. Fish	3/21/41	6	Crusted	0.8	0.9	0.9	0.6
S. Londo	3/ 5/41	10	Dry	0.7	....	....	....

TABLE 9. Light transmission through snow, laboratory experiments, 1941. The source of light was an incandescent bulb.

Date, 1941	Snow Condition	Depth, inches	Percentage Transmission			
			No filter	Red	Green	Blue
Feb. 22	Somewhat wet	½	13	....	....	....
		1	1.1	....	....	....
		2	0.54	....	....	....
		4	tr.	....	....	....
Mar. 23	Fairly dry; lumpy	1	3.4	....	....	....
		2	1.1	....	....	....
		3	0.21	....	....	....
		4	tr.	....	....	....
Mar. 23	Dry; screened	1	5.6	2.5	3.3	4.0
		2	0.81	1.1	0.72	tr.
		3	0.04	0.15	0.14	0.0
		4	tr.	tr.	tr.	0.0

be reduced to a fraction of 1 percent at depth of one meter.

It has been demonstrated that, as a rule, the diminution of the intensity of light in its passage through water follows a definite mathematical formula, the relationship between the depth of water and the amount of light penetrating to that depth being such that it may be plotted as a straight line on semi-logarithmic paper[3] (Clarke 1939, p. 27). The slope of that line is an index of the relative transparency of the water. Many examples of this relationship have been presented by Clarke, by Birge & Juday (1929), Utterback (1941), and others.

The penetration of light through the ice-covered waters of some of the lakes of this study is plotted in this manner in Figure 28 (this figure is explained more fully below). Quite evident are the comparative rapidity with which the colored water of Bog Lake absorbed light, the moderately good transmission through the rather clear waters of Clear and East Fish Lakes, and the extremely low absorption of light in the water of Crater Lake (data from Utterback et al. 1942).

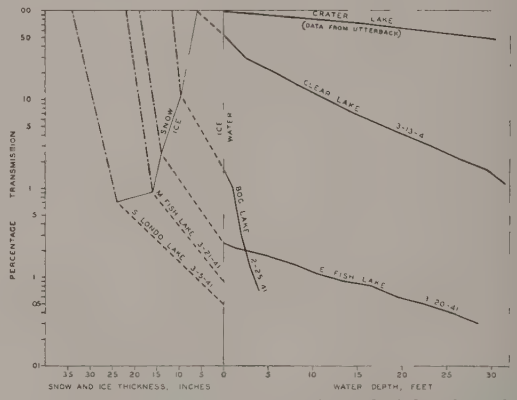

FIG. 28. Percentage transmission of light through snow, ice, and water. Various lakes. See text for explanation of diagram.

As indicated in the papers cited above, there are very large differences in the relative transmission, through water, of light of different spectral qualities. These differences depend in kind and amount upon the type of water. In distilled water, or other very clear water, such as that of the Sargasso Sea, penetration is best effected (within the range of visible light) by blue light, and progressively less well by green, yellow, and red light.

In slightly less clear water, such as that of the clearest inland lakes in Michigan, light in the green or yellow-green portion of the spectrum is transmitted in the greatest amount, red light in the least, and blue light to an intermediate extent. In moderately clear lakes, penetration is greatest in the yellow-green, and considerably less in both the red and the blue. As shown in Figure 29, the water of East Fish Lake was found to have these characteristics.

[3] In many lakes, however, certain conditions, such as differences in the amount of suspended material at various depths, may cause more or less irregular variations in the transparency of the different layers of water (see Whitney 1938, Chandler 1942, and others).

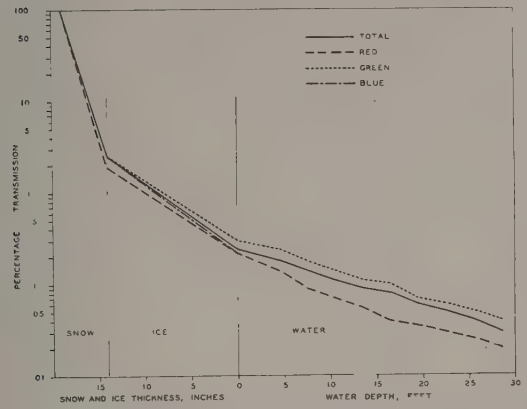

FIG. 29. Percentage transmission of light of different wave lengths through snow, ice, and water. East Fish Lake, March 20, 1941. "Total" light is diffuse daylight as recorded by a Weston cell.

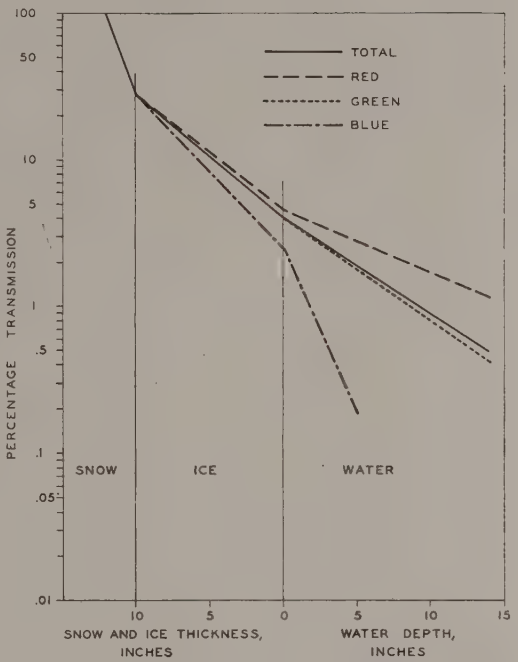

FIG. 30. Percentage transmission of light of different wave lengths through snow, ice, and water. Bog Lake, March 13, 1941.

In the less transparent waters there is a shift toward greater relative penetration in the longer wave lengths (yellow, orange, and red), and in waters of very low transparency, such as highly colored bog waters, the transmission of red light is many times as great as that of green light, and blue light is almost entirely excluded. This differential penetration in colored water is illustrated by Figure 30, which shows the relative spectral transmission through the water of Bog Lake. It is probable that the relatively slight ability of light of the shorter wave lengths to penetrate bog water depends in some way on the presence of suspended particles, since water which is turbid because of suspended silt exhibits the same property (Higgins 1932, p. 523).

In addition to the loss of light in the water itself, there is, in open water, a surface loss, sometimes amounting to a considerable portion of the total light. According to Clarke (1939), only a small part of this loss actually is due to reflection; the remainder is caused by a proportionately high rate of extinction in the uppermost layer of water.

Since all of the observations of the present study pertained to water which was covered with ice, it is difficult to assign any value for "surface loss." In making a measurement of the light penetration through the ice, the target of the photometer was held tightly against the under surface of the ice. However, since there was a small space between the top of the target and the Weston cells, and since ice normally rests in, rather than above, the water, it is apparent that the actual water-ice interface was above the cells. Therefore any loss which this interface, per se, may have caused would have been calculated as part of the loss in transmission through the ice. It seems probable that such loss was small.

Furthermore, the existence and amount of any extra loss in the uppermost thin layer of water, under the ice, is difficult to estimate. The difficulty of accurately gaging the depth of the target (within the first one or two feet below the ice), combined with the possibility of error caused by stray light from the side, prevented the precision of measurement necessary to determine the exact behavior of the water immediately under the ice. Another possibility about which only speculative statements can be made is that of reflection of light back into the upper water from the under surface of the ice (or of the snow).

In general, on the basis of the data as they appear in Table 6 and in Figures 28 and 29, it was apparent that there was no very great difference in the percentage absorption of a given thickness of water in the upper layers as compared with the same thickness in the deeper layers. The slight tendency toward such a difference in Bog Lake possibly can be accounted for by the greater amount of suspended material in the upper water.

TRANSMISSION THROUGH ICE

Of much greater and more striking effect in absorbing light is the cover of ice and snow. The measurements made of light transmission through snow and ice are given in Tables 6-9. Table 7 is a summary of the percentage transmission through ice of various thicknesses and conditions, arranged in descending order of percentage. The values ranged from 84 percent, for 7½ inches of very clear ice, to 2.0 percent for 15 inches of partly cloudy ice.

The figures in this table compare fairly well with the few data which are to be found in the literature. Sauberer (1938) found the transmission through 25

mm. (1 inch) of clear ice to be about 84 to 87 percent, and through 4 cm. (1½ inches) of "schneeis" to be about 45 percent. The figures given by Croxton, Thurman, & Shiffer (1937) are: 4 inches, 86 percent; 6 inches, 66 percent; and 14 inches, 33 percent. Zinn & Ifft (1941) gave the result of only one measurement; through 4½ inches of ice, with a "slush cover," approximately 65 percent of the incident light penetrated. Chandler (1942) found 58 percent transmission through 40 cm. (16 inches) of ice, a percentage transmission equivalent to that through the same depth of Lake Erie water with a turbidity of about 20 p.p.m. The data of these various writers were obtained by the use of instruments and techniques which varied somewhat with each other, but in general they probably are properly comparable.

It is readily apparent (from Table 7) that the penetration of light through ice varies greatly with the condition of the ice. For example, 7½ inches of clear ice transmitted 84 percent, as against 22 percent for 7½ inches of "partly cloudy" ice. Only 7.2 percent of the incident light passed through 10¾ inches of ice described as "very cloudy." This ice was full of minute air bubbles, which gave it somewhat the appearance of opal glass, and rendered it probably as opaque as any ice likely to be encountered on natural waters, except that which might have inclusions of dirt or other foreign matter. Similarly, the "clear" ice just mentioned was probably as crystal-clear as any which ever freezes on inland lakes. Between these two extremes, the ice of most lakes varies greatly in character, and in ability to transmit light, depending on the manner in which it was frozen, on various thraws and refreezings, and so forth. The approximate range of percentage transmission through various types of ice is delimited by Table 7.

As with water, it is probable that a part of the total loss of light in passing through ice consists of "surface loss." For ice this loss is largely undefined and unmeasured. If the usually rather dark appearance of the ice on a lake (especially if the ice is clear) may be used as a criterion, surface reflection apparently is of relatively small amount, and it is probable that most of the total loss actually occurs within the ice. At any rate, and of necessity, the data given here in regard to light absorption by the ice include whatever loss may take place both at the upper surface of the ice and at the water-ice intersurface.

It is assumed that the transmission of light through ice, if the ice is uniform in character throughout, probably takes place according to a mathematical relationship such as that described above for water. Following this assumption, the points on the graphs of Figures 28-30, representing the percentage amount of light entering the ice and that emerging from it, respectively, are connected with a straight line, the slope of that line indicating the relative light-absorbing power of the ice. Comparative lines of this sort have been drawn, in Figure 28, for several of the lakes studied.

The transmission of light through ice apparently varies somewhat with the region of the spectrum. As stated by Dorsey (1940, p. 398), ice in large masses has a blue appearance, probably caused by light scattering. Sauberer (1938) found very little difference between the various spectral bands, in transmission both through clear ice and through "schneeis." In the data of Table 7, the clearer ice showed no significant differences in relative transmission of light of different colors. However, the more turbid ice showed a pronouncedly lower relative penetration of blue light. Apparently, therefore, a proportionately large loss of blue light is associated not so much with pure ice as with included particles, such as air bubbles, or possibly (in the case of the ice of Bog Lake) particles of coloring matter which may have become frozen into the ice. In Figures 29 and 30, the slightly different slopes of the lines for the transmission of various colors through the ice of East Lake and Bog Lake are evident.

TRANSMISSION THROUGH SNOW

The penetration of light through snow is considerably harder to measure accurately than that through ice or water, not only because of the difficulties of making observations under natural conditions (i.e., without disturbing the snow), but also because of the exceedingly many variations in the character of the snow. However, the information obtained is of value in establishing a general range for snow, and thus in showing the relative absorption by snow, ice, and water.

With the exception of one series of experimental determinations, the measurements of light transmission through snow made during the course of this study were performed on the ice of various lakes, without disturbing the natural snow cover. Thus they are of necessity indirect measurements; that is, the value was calculated from the transmission through snow plus ice, compared to that through the ice alone, after the snow had been removed. Probably the only significant error, however, is that caused by surface loss from the ice (see above), and this loss likely is small.

Kalitin (1931) made an extensive series of measurements by placing the target of a photometer on an open field, and allowing the natural snowfall to cover it. The chief difficulties in interpreting the data so obtained lie in the variations in amount and quality of light from time to time, and the changes in the character of the snow between readings. Most of the remainder of the few observations which have entered the literature have involved some sort of an artificial set-up, with consequent disturbance of the snow. However, in spite of variations in procedure and apparatus, the measurements made by the various writers may be used to form a general idea of the light-transmitting qualities of snow.

The reflection of light from the surface of snow is

very much greater than that from water or ice. The albedo, expressed as the ratio of reflected light to total incident light, varies, according to the tabulation by Dorsey (1940, pp. 486-487), from 40 or 50 percent to over 90 percent. Thams (1938) gave for new snow 82 percent, for old snow 60 percent, and for melting snow 50 percent. Sauberer (1938) found new snow to have an albedo of about 84 percent, and old snow about 72 to 76 percent. The figures of Kalitin (1930, 1931) range from 52 percent for old, grainy snow, to 87 percent for fresh, dazzling white snow. Considerable and rapid changes were noted by this author. After experimental wetting of the snow surface, the albedo was 52 percent. Hand & Lundquist (1942) gave values up to 89 percent for clean white snow.

In the measurements of this investigation (Tables 6, 8, and 9), separate account was not taken of the loss from the snow surface; the figure given in each instance is that for the amount of light which emerged from the bottom of the snow layer, expressed as a percentage of that incident upon the upper surface. Stated as true percentage transmission through the snow, the ratio would be larger. However, since the concern of this study is with the amount of light ultimately passing through the sequent snow, ice, and water, the amount of loss by reflection at the surface of the snow is of interest chiefly in helping to explain the tremendous power of snow to reduce light intensity.

In Table 8 are summarized the snow transmission measurements on the various lakes. Percentage transmission varied from 28 percent for 1 inch of slushy snow, to 0.7 percent for 10 inches of dry snow. Crusted snow apparently allowed somewhat less penetration than light, dry snow.

Table 9 shows the percentage transmission through snow artificially placed on the photometer target. A thickness of 1 inch permitted only about 4 or 5 percent of the light to pass through it; at 4 inches only a slight trace of light remained. These figures are subject to the possible error caused by the use of light of relatively low intensity (incandescent bulb); the transmission percentages thus may be proportionately somewhat low (see reference, below, to Croxton et al.).

Figures from the literature are somewhat scattered. Thams (1938) recorded 13 percent transmission for 10 cm. (4 inches) of snow, and 0.6 percent for 50 cm. (20 inches). These figures are somewhat high as compared to those of other workers. The transmission found by Croxton, Thurman, & Shiffer (1937), using snow artificially placed above the photometer, varied from 11.7 percent for 1 inch, to 0.03 percent for 7 inches. These latter writers found a lower percentage transmission for light of low intensity, and considerable differences caused by differences in the quality of the snow. Clean and fresh snow allowed the greatest penetration, clean but wet snow the next greatest, and granular snow the least. This order agrees with the findings of Hand & Lundquist (1942), that within a certain range the higher the water content of the snow the less light transmitted. The figures given by Hand & Lundquist, for "fine granular compact" snow, range from 22.3 percent for ½ inch, to 1.2 percent for 5¾ inches. Kalitin (1931), in a table of summary, gave percentage transmissions ranging from 21.7 percent for 2.5 cm. (1 inch), to 0.09 to 0.03 percent for 62 cm. (about 24 inches). Again wet snow was found to transmit light less freely than did dry snow.

It is not certain in all cases, but apparently all of the figures given above were based upon total amount of incident light (rather than upon that remaining after surface reflection loss), as also are the figures of the present study. That means, then, that wet snow transmits less of the total incident light than dry snow, in spite of the fact that dry snow has a higher loss by surface reflection.

Figure 31 shows the relative light-transmitting properties of snows as measured by various observers. The assumption is made that a logarithmic relationship holds between depth of snow and percentage penetration. This assumption has been made by Sauberer (1938), who gave an actual absorption coefficient. If the assumption is true, then the relative slope of the lines on Figure 31 give an indication of the relative powers of these various snows to absorb light.

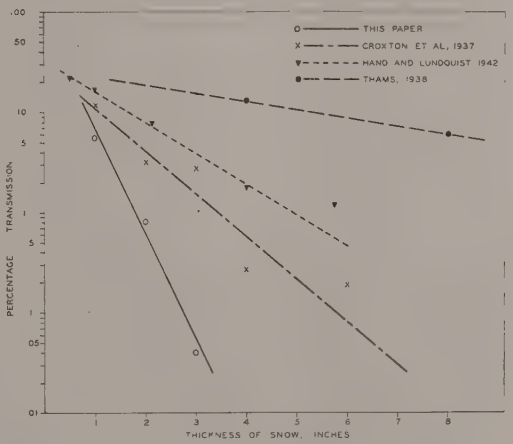

FIG. 31. Percentage transmission of light through snow. Data from authors.

Each of these lines, produced to the axis of the graph, would intercept the axis below the 100 percent mark. The difference, presumably, represents that part of the light which was lost in surface reflection.

Figure 28 is a composite diagram of the combined effects of snow, ice, and water in diminishing light intensity. Starting at 100 percent of incident illumination, each line shows, first, the drop in intensity caused by the snow, next the further drop in passing through the ice, and finally the diminution caused by the water. The plotted value for percentage inten-

sity at any point on the line represents, theoretically, the amount of light penetrating to that particular depth of snow, ice, or water. The line for Crater Lake (based on data from Utterback, Phifer, & Robinson 1942, and Brode 1938) does not include ice, since the water was open at the time of observation.

The tremendous differences in the amount of light reaching various depths under different conditions of snow and ice are apparent from the figure. For example, for the dates given for the respective lakes, Clear Lake received more light at the 32-foot depth (1.1 percent transmission) than did Bog Lake at 1 foot under the ice, and 22 times as much as South Londo Lake just under the ice (0.05 percent). The light penetrating to the bottom of East Fish Lake (under the given set of conditions) was only 0.03 percent of that which reached the top of the snow cover. That percentage transmission was only about one-fourth as much as that to a depth of 120 meters (about 400 feet) in Crater Lake (data from Utterback et al. 1942).

In terms of foot-candles of light falling upon the target of the photometer (see under Methods), a few sample readings, taken from Table 6, are: of 7,600 foot-candles falling upon the snow on South Londo Lake (March 5, 1941), only 4 f.c. penetrated the ice plus snow. At Clear Lake (February 23, 1941) an incident illumination of 8,000 f.c. resulted in the penetration through the ice of 6,700 f.c., or 84 percent, and to the bottom of the lake (30 feet) of 112 f.c., or 1.4 percent. Thus 1,700 times as much light penetrated 7½ inches of clear ice with no snow (Clear Lake) as was transmitted through 24 inches of partly cloudy ice covered with 10 inches of snow (South Londo Lake).

The transmission of light through snow apparently varies somewhat with the region of the spectrum. Sauberer (1938) found the relative penetration to be the greatest in the green-yellow portion of the spectrum, and to fall off in the blue and slightly in the red. Kalitin (1931) stated that absorption of light by wet snow is greatest in the longer waves (the red). The somewhat scanty data of the present study (Tables 8 and 9) apaprently show a somewhat reduced penetration in the red and blue spectra.

RELATION TO PHOTOSYNTHESIS AND DISSOLVED OXYGEN

In spite of considerable work by various investigators, comparatively little exact information is available regarding the quantitative light requirements of aquatic plants under various conditions. It is extremely difficult, in measuring these requirements, to control all of the necessary factors. It is evident, however, that for any given set of conditions there must exist an intensity of light which will promote photosynthesis, and below which photosynthesis will be overbalanced by respiration. Such an amount of light has been termed the compensation intensity.

Clarke (1939) cited references which placed the compensation intensity (plant species and other factors not stated) at about 350 to 500 lux (approximately 30 to 45 foot-candles). Wilson (1935) found the lower limit of certain types of aquatic vegetation, in a lake in Wisconsin, to be at a depth at which the light amounted to from 4.4 to 6.8 percent of the "total sunlight at zenith"—that is, at roughly 400 to 600 foot-candles. It seems likely, however, that factors other than light intensity also operated to limit the maximum depth of growth of these plants. Pearsall & Ullyott (1934) found rooted vegetation to be adversely affected when the light intensity was cut down from about 4 or 5 percent to about 1½ or 2½ percent.

Little is known about the light requirements of the phytoplankters of inland lake waters. Probably there are considerable differences among the various species, and such factors as temperature must have a certain effect. However, some of the figures given in Table 6 for the amount of penetration of light through snow plus ice cover are such small fractions of the amounts proposed as general aquatic plant compensation intensities, that it seems almost certain that such small amounts of light could not maintain a favorable balance of photosynthesis over respiration and decay. On the other hand, there appears to be reason to suppose that the amount of light which penetrates even 1½ to 2 feet of moderately clear ice (with no snow cover) is enough to satisfy the requiremenst for photosynthesis.

Photosynthesis is controlled to a large degree by the quality, as well as the quantity, of light. In general, red light is more effective than that of shorter wave lengths. Some aquatic plants, however, such as certain diatoms, have been found to be able to utilize almost any part of the visible spectrum (Jenkin 1937). As discussed above, there are certain differences in the transmission of light of various wave lengths through ice and snow. However, in general these differences are relatively small, and it is probable that the more important effect of the ice and snow is that of reducing the total quantity, rather than of changing the quality, of light.

The measurements of light penetration made during this study were too limited in number to justify any attempt to show a correlation between light intensity and oxygen production which would be expressible as a mathematical function. However, as is discussed above, a definite connection is demonstrable between the dissolved oxygen in the water and the amount of snow on the ice; and in this manner the effect or the oxygen tension of the water of changes in the light intensity on the oxygen tension of the water is clearly shown. It appears conclusively evident that a heavy snow cover upon the ice so greatly reduces the amount of light entering the water that photosynthesis by the phytoplankton virtually ceases, with a consequent and almost certain reduction in oxygen production.

EXPERIMENTAL STUDIES

PUMPING EXPERIMENTS, PREVIOUS WORKERS

Experimental aeration of water under the ice has been attempted by various workers. In Iowa, in 1935

and 1936, air blowers were used (Aitken 1938). These blowers delivered a large volume of air, under fairly low pressure, into the water. They were not very successful, however. Presumably a relatively small part of the air actually went into solution in the water. In the same state in 1936-37, pumping water into the air was tried, the object being for this water to absorb or entrap air and carry it back into the lake. The method was held to be impractical for aerating large lakes.

Various pumping procedures have been tried in Minnesota and Wisconsin. Some small success attended the experiments in which a stream of water and one of compressed air were mixed at the point of entrance into the water. However, here again it was found that the method was not suitable for aerating large bodies of water.

In Michigan, during the severe conditions of the winter of 1935-36, the Institute for Fisheries Research attempted experimental aeration by means of a stream of water pumped from the lake, sprayed into the air, and allowed to return through holes cut in the ice. This experiment has been referred to by Hubbs & Eschmeyer (1938). Although the water at the point of entrance through the ice was found to have a very much increased oxygen content, this increase was transitory, and disappeared within 28 hours. Furthermore, the effect was very local, indicating the method to be of small value for application to any considerable area.

PUMPING EXPERIMENT, PASINSKI'S POND

Pasinski's Pond was used, in February and March, 1940, for an experiment in aeration by means of a pumped stream of well water. The pond is described above; Figure 6 is a map showing its outline, depth contours, and the location of sampling stations. Although the pond is one simple basin, it has been found convenient to divide it, for the purpose of interpreting certain data, into two parts, the north end (containing the pump) and the south end (including the outlet). This division is based upon the vegetation present. The south end contains large beds of filamentous algae (principally Spirogyra), as well as an almost solid mat of Anacharis. Algae are practically absent from the north end, which has, however, a fair amount of Anacharis. These weed beds of course are more distinctly to be observed during the summer months.

At the start of the winter of 1939-40, only one sampling station was used (Station 15, in the north end). This station was about 75 feet from the point of discharge of the pump. The dissolved oxygen at this station (the surface sample) dropped rapidly and steadily, from 19.1 p.p.m. on January 7, to 0.5 p.p.m on February 10 (see Figure 32).

On February 10 the pump was set into operation, pumping about 60 gallons per minute. The well water as it came from the pump carried only about 1.5 to 2.0 p.p.m. of dissolved oxygen, but by running through wire mesh and over an inclined trough it increased its oxygen content to about 4 to 6 p.p.m.

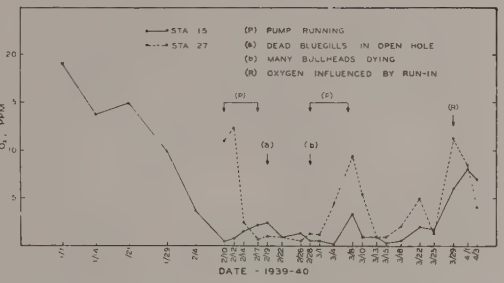

FIG. 32. Dissolved oxygen, effect of pumping water. Pasinski's Pond, Station 15 (north end) and Station 27 (south end). Surface samples, 1939-40. See text.

Its temperature was approximately 50° F. (10° C.).

The pump was operated continuously for seven days, until February 17. During that time the discharge from the pump melted a hole through the ice at the edge of the pond, roughly 8 or 10 feet in diameter. This hole remained open during the time that the pump was running, and for two or three days afterward; it constituted the "open hole" to which reference is made elsewhere in this paper.

On February 10, about 25 stations were established, in a sort of geometric design, in the north end of the pond, and three stations in the south end. A few more stations subsequently were added. Samples were taken at these stations, at intervals of from two to four days, from February 10 until April 1. Uniformly, the samples were surface samples, except that enough check samples were taken from other depths to show that the highest oxygen values always were to be found in the upper water (see discussion, below, on dissolved oxygen consumption in lakes).

After having run for seven days, the pump was turned off on February 17. It was started again on February 28, and ran continuously until March 6.

The original idea was to use the south end of the pond as a control, to determine the amount of aeration accomplished in the north end by the pump. This plan was found to be faulty, however, since initial conditions in the two ends of the pond were different. Presumably because of the activities of the algae in the south end, the water there had much more dissolved oxygen at the start of the experiment than did that at the north end.

The dissolved oxygen data of the experiment are not amenable to most methods of statistical treatment. Average values are scarcely valid, since there was much fluctuation between stations, and also since too few stations in the south end were used. However, Figure 32 is of some help in interpreting the possible effect of the pump. On this figure are shown the dissolved oxygen values for Station 15 (north end) and Station 27 (south end). In accordance with the above explanation, these two stations do not necessarily represent the average values of the two ends of the pond, but they may be considered somewhat typical.

At the time the pump was first put into operation, on February 10, the oxygen was much higher at Station 27 than at Station 15, but was declining rapidly at Station 27. Either under the influence of the pumping or for some other reason, the oxygen gradually increased at Station 15 until February 19. when it was 2.4 p.p.m.; meanwhile that at Station 27 had gone down to a low of 0.7 p.p.m. on February 17. From February 22 until March 1 the oxygen remained quite low at nearly all stations in the pond, in spite of the fact that the pump was again put into operation on February 28.

From March 1 until March 4 there was a rise in the oxygen at Station 27, as well as at other stations in the south end; while the oxygen at Station 15 and at most other stations in the north end still remained low, in spite of the pumping. Then, from March 4 until March 8, there was a sharp increase in oxygen at both ends of the pond. As shown by the curves of Figure 32, this increase was larger and began earlier in the south end. It probably was due to renewed photosynthetic activity, since nearly all of the snow by this time had left the ice. The south end of the pond, containing more algae, responded much sooner and to a greater extent to changes in light intensity than did the north end.

The peak values on March 29 presumably were occasioned in part by inflowing water from rain and melting snow.

There is further evidence that the pumping had very little if any beneficial effect. On the sampling dates during the first period of operation of the pump, February 10 to 17, only seven samples of all those taken in the north end (Stations 1 to 23) had 2.0 p.p.m. or more of dissolved oxygen. None had over 2.8, and most of them ranged from 0.2 to 1.5 p.p.m. Of the samples from the ten stations nearest the pump, only two had 2.0 p.p.m. or more, and oxygen values as low as 0.3 p.p.m. were found within 20 feet of the discharge point of the pump after four days of operation.

Pumping 60 gallons per minute, or about 11,000 cubic feet per day, the pump would displace approximately one-fortieth of the volume of the pond per day (assuming that the pumped water did not set up a current which would shunt it to the outlet). If the pumped water, containing about 5 p.p.m. of dissolved oxygen, became completely mixed with the pond water, it could (theoretically) raise the oxygen content of the entire volume of water approximately one-fortieth of 5.0 p.p.m., or about 0.125 p.p.m., per day,[4] or about 0.9 p.p.m. on 7 days. Or if it is arbitrarily assumed that only (say) the northern one-third of the volume of the pond were affected, then the oxygen content at that end could be raised about 2.7 p.p.m. in 7 days.

It is quite evident that no such increase took place during the period February 10 to February 17. Presumably the explanation lies in the high oxygen demand which had been built up in the water. Very little oxygen, if any, was being produced by photosynthesis in the north end of the pond, and an oxygen demand existed which could not be overcome by the efforts of the pump.

If the pump were operated for long periods of time (a somewhat expensive and troublesome procedure) it probably would be of considerable help in forestalling the development of serious conditions. But once those conditions have developed in the pond, pumping well water apparently is almost useless.

On February 14, four days after the pump first was started, there were several bluegills in the open hole, alive but not very active. On February 19, two days after the pump was turned off, the open hole contained hundreds of dead bluegills. Mortality struck suddenly, for on February 17 there were few if any dead fish. Apparently all or most of the bluegill population died within a few days, for no dying or newly dead bluegills were observed during March.

The bullheads began to die somewhat later than did the bluegills. Very few dead bullheads were seen in early February, but on February 28 many were dead or dying. The mortality of the bluegills apparently was complete, for intensive seining the following summer failed to take any. Only a part of the bullheads died. Altogether some 13,000 bluegills and over 1,000 bullheads were killed.

SNOW REMOVAL, HATCHERY PONDS

Three of the small experimental ponds at the Drayton Plains hatchery were used for the experiment here described. Early in December, 1939, these ponds were filled with water from the river, to a depth of about 2½ feet. In order to maintain the water level, a small flow was permitted to run into and out of each pond. This flow remained somewhat larger than was intended, and affected the results of the experiment to a certain extent. However, the flow was about the same in each pond.

The three ponds were allowed to remain undisturbed, except for the taking of samples, until February 12. On that date the snow (about 3 inches in depth) was shovelled cleanly off the ice of Pond 10. From that time on, the snow was removed from this pond soon after each new snowfall.

On February 17 the ice on Pond 8 was completely covered with a layer of opaque building paper, which was held in place with snow. The paper stayed in place very well until the breakup of the ice.

Pond 9 was left unmodified throughout the experiment, as a control.

From January 7 until the breakup of the ice, dissolved oxygen samples were taken periodically in all three ponds. The sampling depth was 1 foot. In Figure 33 are shown the dissolved oxygen curves.

In view of the fact that the three curves stayed so closely together until the beginning of experimental conditions, their divergence after that time seems to be definitely significant. Evidently the amount of light entering the water did have an appreciable effect

[4] Obviously the pumped water, carrying only 5.0 p.p.m. of oxygen, could increase the oxygen in the pond water only if the latter had less than 5.0 p.p.m. to begin with; and the full amount of the increase given in the computations above could come about only if the pond water had zero oxygen at the start.

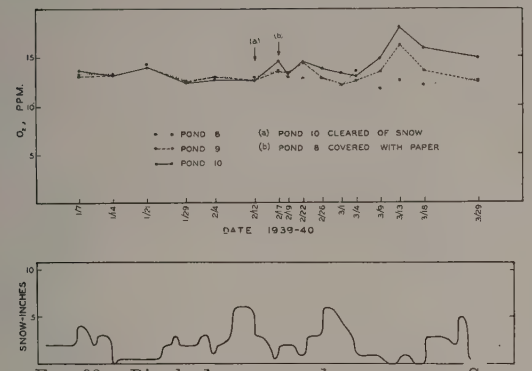

FIG. 33. Dissolved oxygen and snow cover. Snow-clearing experiment, hatchery ponds, 1939-40. See text.

upon the dissolved oxygen. It is only reasonable to suppose, furthermore, that this effect would have been much greater had there not been a continuous partial displacement of the water.

It seems probable that the differences between the curves for the three ponds were not due so much to diminution of oxygen in Pond 8 (probably the inflowing water carried enough oxygen to satisfy the relatively small oxygen demand present), as to the greater oxygen production in Ponds 9 and 10. The amount of light entering Pond 9, through the snow-covered ice, apparently was enough for some photosynthesis (it must be remembered that for a time in early March the ice of Pond 9 was bare or nearly so), and the water in Pond 10, with the snow removed, received more light and did still better in oxygen production.

SNOW REMOVAL, GREEN LAKE

On January 22, 1943, the snow on a roughly measured one-acre area of Green Lake was melted down by means of a stream of water pumped from beneath the ice. For this work a centrifugal pump was used, with a capacity of about 3,000 gallons per minute, and driven by an air-cooled gasoline motor. The intake pipe of the pump was thrust through a hole in the ice, and the outflow took place through a 2½-inch rubber-lined canvas hose about 20 feet long. In order to cover the area, which was rectangular, roughly 300 feet by 150 feet, the pump had to be moved from one position to another about 8 or 10 times. Laying off the plot, chopping holes for the pump, and performing the actual pumping took two men about 7 to 8 hours.

Part of the time the water was sprayed onto the surface of the snow in a very coarse spray, and part of the time it simply was allowed to run from the open end of the hose out onto the ice, through and under the snow. The former method was only slightly more effective, and involved more effort than the latter.

At the time of the pumping, the snow over most of the lake was from 8 to 10 inches deep, including the slush, which came in most places to within 3 or 4 inches of the surface of the snow.

No effort was made to completely melt the snow to water. Rather, it was only wet down into a thin slush. The difference in appearance between the treated and untreated areas is shown in Figure 34. The slush formed by the pumping subsequently froze into firm, although rough and somewhat cloudy, ice. As has been mentioned above, even cloudy ice has many times the light-transmitting ability that snow has.

It was intended, of course, that the untreated area would serve as a control, and that parallel oxygen determinations in the days following the experiment would show the effect, if any, that the melting of the snow had on the dissolved oxygen. However, in the two days from January 22 to 24 the snow over most of the lake virtually disappeared, through natural causes. A few small local areas retained from ½ to 2 inches of snow for a few days, and some of these

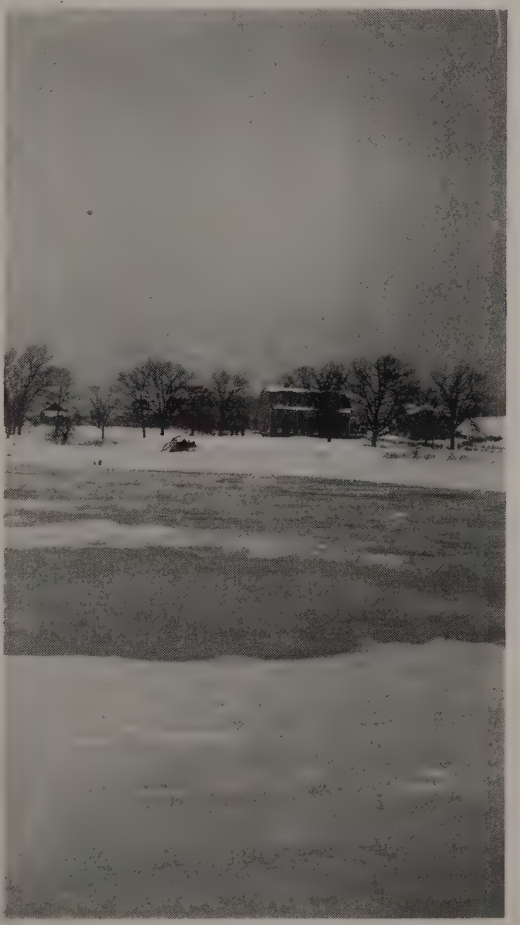

FIG. 34. Contrast between flooded and nonflooded areas in the snow. Green Lake, January 22, 1943.

were utilized for oxygen determinations, but to all practical intent the desired control was lacking.

Dissolved oxygen figures (averages) for several stations within and outside of the treated area, on three sampling dates following the experiment, are given in Table 10. These data show an apparent slight trend for the oxygen to be higher in the treated area than outside of it. Because of the circumstance just described, however, no significance can be attached to this seeming difference. Furthermore, even within the treated area the oxygen declined somewhat in the ten days after the pumping. Thus if the light which penetrated the ice actually was sufficient to produce oxygen, it was not capable of quickly overcoming the serious oxygen-depleting conditions which had arisen.

TABLE 10. Snow removal experiment, Green Lake, 1943. Dissolved oxygen, p.p.m., average values for stations within and outside of treated area. Number of stations averaged and range of values, in parentheses.

Date	Surface Sample		2-Foot Sample	
	Inside	Outside	Inside	Outside
1/22*....	(4) 5.2 (4.2–6.4)	(1) 6.1	(1) 2.5	(1) 2.5
1/24.....	(10) 6.4 (4.3–11.2)	(7) 4.6 (3.2–7.2)	(7) 3.1 (1.8–4.9)	(7) 1.7 (0.6–2.3)
1/29.....	(10) 3.8 (3.0–4.7)	(7) 2.9 (2.0–3.8)	(7) 2.5 (2.1–2.8)	(7) 1.9 (1.1–3.1)
2/2.....	(5) 3.2 (2.8–3.7)	(5) 2.3 (1.1–3.7)	(3) 2.1 (1.8–2.3)	(5) 2.0 (1.0–3.0)

*Before pumping, January 22.

By about February 5 the lake as a whole apparently had reached its low point (as regards dissolved oxygen), and recovery from that time on was general and fairly rapid. There was no appreciable amount of snow on the ice most of the remainder of the winter.

THE OXYGEN BALANCE OF AN ICE-COVERED LAKE

The relative abundance or lack of dissolved oxygen is so definitely a controlling factor in the life processes in an ice-bound lake that careful consideration should be given to the various agents which act to lower or raise the dissolved oxygen content. The following discussion attempts to collate some of the information to be found in the literature, as well as certain observations of the present study.

Two diametrically opposed sets of processes exist and usually are concurrently active—those which consume oxygen, and those which replenish it. The precarious balance between the two is fine indeed, and when this balance is upset the consequences may be sudden and intense. The action of these processes is greatly influenced by the low temperature of the water in winter. Also it is limited considerably by the ice cover, and by the almost complete immobility which arises from thermal stratification and lack of wind agitation. Except for these modifications, the processes of oxygen utilization and oxygen renewal are in general the same processes which exist in the summer.

Oxygen Consumption

RESPIRATION OF FISH

It is a rather common concept that the respiration of the fish is a chief factor in the diminution of the dissolved oxygen. In occasional instances this may be true. Some bodies of water, such as pot-holes, rearing ponds, and so forth, may have an extremely high concentration of fish. Kochs (1891) estimated the fish in certain wintering ponds to amount to 1 to 1½ kilograms per cubic meter of water, which is roughly equivalent to 2,700 to 4,000 pounds per acre-foot. Certainly such an amount of fish would consume an appreciable quantity of oxygen, even at winter temperatures. However, such quantities are rather exceptional. The concentrations of fish in lakes such as those of the present study are on the order of a few hundredths of the extreme figure given above. Even in organically rich, shallow ponds of this region, probably a standing crop of 75 to 100 pounds per acre-foot is very rarely exceeded.

There is scant information available concerning the oxygen requirements of fish at near-freezing temperatures. Some of the data of the literature are summarized in Table 11. Probably the average value for the warm water fishes commonly found in southern Michigan waters (such as black bass, sunfish, suckers, yellow perch, etc.), for the temperature range 0°-4° C., is somewhere between the highest and lowest of the figures given in this table.

TABLE 11. Oxygen requirements of various fishes at low temperatures.

Fish	Temp., °C.	O_2 consumed, cc./kg./hr.	Author
Brown trout.....	4–7°	102.5	Gardner & Leetham (1914)
Goldfish.....	2°	14.8	Regnard (1891)
Goldfish.....	5–6°	16.07	Gardner & King (1923)
Tench.....	0°	6.05	Linstedt (1914)
Pike (*Esox lucius*)....	5–6°	24.44	Gardner & King (1923)
Eel.....	5–6°	9.28	Gardner & King (1923)

For purposes of comparison, it is perhaps of interest to make a rough theoretical computation of the amount of oxygen used by the fish in a given body of water. During the winter of 1939-40 Pasinski's Pond had an average volume, excluding ice cover, of approximately 350,000 cubic feet (9,900 cubic meters), or about 8.0 acre-feet. This amount of water weighs 22,000,000 pounds. If it were saturated with dissolved oxygen, at 0° to 4° C. (i.e., with about 14 p.p.m.), the water in the pond would contain about 300 pounds of dissolved oxygen. Suppose there were in the pond 500 pounds of fish (62.5 pounds per acre-foot). This is a hypothetical figure, and probably is too high. Using the also hypothetical figure of, say, 25 cc./kg./hr. (equal 0.000036 lb./lb./hr.) for the average oxygen consumption of the bluegills and bullheads in the pond, the figure obtained for the oxygen used by the fish is 0.018 pounds of oxygen per hour, or 0.43

pounds per day. At that rate, 300 pounds of dissolved oxygen would meet the respiratory needs of the fish for 700 days (actually, of course, the fish would be unable to utilize the last of the oxygen, because of their inability to extract it at low tensions).

In comparison, Kochs (cited above), using the value given by Regnard of 14.8 cc. of O_2 per kg. of goldfish per hour, and the (slightly too low) figure of 10.58 p.p.m. for dissolved oxygen at saturation, obtained the theoretical result that the water in the carp wintering ponds which he was studying held only a 20-day supply of oxygen for the fish.

It seems rather certain that in the average Michigan lake of the winter-kill type the fish play a very minor part in the depletion of the dissolved oxygen under the ice. The respiration of other aquatic vertebrate animals also has little influence upon the oxygen supply, since most of them, with the exception of tadpoles and immature salamanders, are air-breathing.

RESPIRATION OF INVERTEBRATES

It is extremely difficult to evaluate properly the part played in the oxygen depletion of a lake by the respiration of invertebrate animals, since the two chief governing factors, the number of organisms present and the oxygen requirements of each, are to a large extent unknown. Especially is this true in the winter.

Comparatively few quantitative studies of winter zooplankton have been made. There is considerable variation from lake to lake and from one winter to another. In general, however, the total zooplankton is usually at a minimum in winter. Very few of the larger zooplankters (copepods, daphnids) have been found to display winter pulses, and these probably are transitory or local. Naber (1933) concluded that the plankton animals perform a very small part of the removal of oxygen from a lake. Considering the small size of these animals, and the reduction in their oxygen requirements brought about by low temperatures, it is likely that their respiration accounts for an insignificant portion of the oxygen consumed during the period of ice cover.

The bottom-dwelling invertebrates usually are more abundant in winter than in summer, since many insects pass the winter as aquatic larvae or nymphs. These immature insects may be present locally in almost prodigious numbers, an example being the concentrations in places in many Michigan lakes, of burrowing mayfly nymphs. Midge-fly larvae often are present in many hundreds or even thousands per square foot of bottom. Since winter is a time of growth and activity for the aquatic insects, they require a certain amount of oxygen, even at low temperatures.[5]

With the exception of an occasional concentration, most other benthic invertebrates are present in much smaller numbers. Relatively large forms, such as crayfish, mussels, or the like, probably are rather lethargic in winter.

No matter what the total oxygen-consuming power of the bottom animals, it is obvious that they can have a direct oxygen-depleting effect upon only the thin layer of water in direct contact with the bottom (the indirect transmission of this effect, as set forth in the microstratification theory, is discussed below). Of the sporadic migrations of bottom dwellers into the upper water, little mention need be made. When occasioned by adverse conditions near the bottom, as they often are, these migrations may be said to represent mainly an effect, rather than a cause, of oxygen diminution.

On the whole it seems probable that, compared to the amount of oxygen used by the decay of dead organic material, that consumed by the respiration of invertebrates is a proportionately small amount.

RESPIRATION OF PLANTS

Living plants, both macrophytes and plankton algae, use oxygen for respiration. Under the proper conditions, these plants produce much more oxygen than they use. When adverse conditions arise, however, oxygen production falls off, and eventually is over-balanced by oxygen consumption. It is difficult to say at what point a plant can no longer be considered to be in a living state, and beyond which its oxygen-consuming process is one of decay rather than of respiration. However, for purposes of present discussion, it is perhaps justifiable to represent most of the oxygen demand of the plants under the ice as being occasioned by their decomposition, whether or not they are in a strict sense dead.

Not usually thought of in the flora of a lake are the actinomycetes of the genus Micromonospora, which have been shown by Umbreit & McCoy (1941) to be rather numerous in several Wisconsin lakes, and which are belived by these authors to play a definite part, although probably a small one, in the dissolved oxygen cycle. Their importance probably lies in the quality, rather than in the quantity, of organic material which they oxidize, since they have the ability to attack such usually resistant materials as chitin, lignin, cellulose, and so forth.

Fungi also often are present in lake water, but it is doubtful that they ever reach sufficient concentrations to be very important as an agent in oxygen depletion. The activities of the water and bottom mud bacteria are discussed in the sections below.

DECAY OF BOTTOM MATERIALS

The role of decomposition of bottom materials in the utilization of oxygen is a very important one, and has been the subject of much discussion. The relative importance of the organic matter in the lake bottom and that suspended or dissolved in the water is somewhat speculative, and various divergent views have been expressed.

It has long been known that in winter, as well as in summer, the water near the bottom of a lake is more apt to be lacking in oxygen than that nearer

[5] It must be remembered that the temeprature on or near the bottom usually is 3°-4° C. higher than that just under the ice, probably a significant amount as related to metabolism. For that matter, inhabitants of the profundal regions of deeper lakes live, the year around, at temperatures only slightly above 4° C.

the surface, and many writers have associated this difference with the decomposition of the bottom mud. In this connection it is of interest to note that, as discussed above, the lines of equal oxygen concentration tend to follow the bottom contour of the lake in their configuration.

Drown (1892) found, in the oxygen content of the water in several ponds in the winter, variations which appeared to have a connection with differences in the composition of the bottom materials, and concluded (p. 341) that "it is the character of the bottom of the pond, rather than the organic matter in solution and suspension in the water, which determines the amount of oxygen remaining in solution." Birge & Juday (1911) observed that the greatest decrease in oxygen, in winter, was near the bottom, and indicated that bottom decay is an important factor. Miyadi (1934) said (p. 236): "It is a recent common opinion to esteem the bottom deposit higher than the decaying plankton organisms sinking down from the epilimnion in diminishing the oxygen of the deep water." And Henrici (1939) made the well-nigh dogmatic statement: "It is the tremendous oxygen-consuming power of the large numbers of bacteria in the lake bottom which . . . causes oxygen to disappear below the thermocline in stratified eutrophic lakes, which causes fish to suffocate in shallow lakes in the winter."

In his microstratification theory Alsterberg (1927) gave the decay of bottom materials as the chief cause of oxygen depletion in the deeper water of a lake, particularly in the thin layer of water lying directly on the bottom. The oxygen lack of this microstratum is gradually transmitted, he believed, into a deficiency in subsequently shallower layers through water movements brought about by wind or otherwise. As Welch (1935, p. 121) has pointed out, this transmission might be produced in an ice-covered lake by the rising of gas bubbles from the bottom or by convection currents. These convection currents under the ice have been held by Mortimer (1941-1942) to produce "turbulent eddies," which tend to diffuse dissolved substances and to transmit to upper layers of water the oxygen reduction which occurs at the water-mud interface.

In regard to the vast potentialities on many lake bottoms for the consumption of oxygen, there can be no question. In the deeper portions of most eutrophic lakes, and indeed throughout the entire area of many shallow lakes, the bottom is heavily blanketed with a soft, semi-organic material variously termed "muck," "peat," "humus," "Schlamm," and so forth. Consisting to a large extent of the dead remains of plants and animals, this material is rich in carbonaceous and nitrogenous substances in various stages of decomposition. The combustible organic matter may constitute as much as 50 percent of the total weight (Birge & Juday 1911; Black 1929; Juday, Birge, & Meloche 1941).

In some lakes and ponds the bottom may be further enriched by the deposition of various other organic substances. Griffiths (1936) considered the partially disintegrated remains of an unusually abundant stand of Nuphar to be a factor of considerable importance in the lowering of dissolved oxygen in a certain ice-covered pool. It is probable that in Pasinski's Pond, in the present study, the rich growth of Anacharis and Spirogyra was at times sufficiently in a state of decay to use a large amount of oxygen.

At times water running into a lake, from fields or in inlet streams, may carry suspended material which settles to the bottom, adding to the organic load. If domestic sewage or other organic pollutional waste is allowed to enter a lake, it may form sludge deposits of great oxygen-consuming power. The danger of adding too much sewage or manure to winter carp ponds has been recognized by Knauthe (1899), Sniezko (1941), and others. The likelihood of the formation of extensive sludge deposits in most natural lakes, however, is small, except in cases of out-and-out pollution.

The mechanics of the decomposition of bottom materials, and the part played therein by bacteria, has been the subject of considerable study. It is well known that bacteria in the bottom sediment are very numerous and diverse. Also, logically, these bacteria are adapted to the utilization of the bottom materials for their food. As is discussed below, many of these forms exist anaerobically, but there are many others which carry on aerobic decomposition when oxygen is available. Naturally, the activities of the bacteria are correlated with the temperature, but a large amount of decay goes on even at temperatures near freezing. Probably some sort of an adaptation may be assumed, since the bottom mud usually is relatively cold the year around.

The amount and nature of the bacterial decomposition depend also to a large extent upon the composition of the bottom deposits. Waksman (1941) divided the organic matter in lake bottoms into (1) readily decomposable constituents, such as carbohydrates and certain proteins, and (2) the more resistant "lake humus" components, such as lignins, and so forth. The organic matter on the bottom of dystrophic lakes has been shown (Henrici 1939) to be much less easily decomposed than that of eutrophic lakes.

ACTIVITIES OF GASES

An important part in the oxygen cycle is taken by the several gases which are generated during the processes of decay of organic matter. These gases, methane, carbon dioxide, hydrogen sulfide, ammonia, nitrogen, and possibly carbon monoxide and others, may be formed in the water, but are more apt to arise in large quantities from the decomposition of bottom muck. Their production comes about principally through the activities of anaerobic bacteria, which are present in the bottom materials in great numbers and many forms. Experiments have shown (Allgeier, Peterson, Juday, & Birge, 1932; Black 1929) that gas production by these organisms is very much slowed down at low temperatures. The former authors found the decomposition to be only about one-fifth as much at 7° C. as at 23°; Black obtained only

about a quarter as much gas from a sample kept at 4° C. as from one at room temperature. The gas produced at 4° was about half methane, the remainder being carbon dioxide, hydrogen, and nitrogen. It is obvious, furthermore, that the amount of anaerobic decomposition which takes place on the lake bottom is closely correlated with the kind and amount of organic material present, just as in the case of aerobic action, and that it may be much higher in sediments of a distinctly sludge-like nature.

The occurrence of these gases of decay in winter-bound lakes has been reported by several writers. Kochs (1891) spoke of the presence in winter carp ponds of methane, amomnia, and hydrogen sulfide, the last of which he believed to be an important agent of oxygen consumption. Under the extremely stagnant conditions found by Knauthe (1899) in a small pond, methane was so abundantly produced that "large bubbles of this harmful gas gathered in the middle of the pond under the ice and . . . the young people of the village found pleasure in boring holes in the ice, and burning the gas at the holes."

During the course of the present study gas evolution was noted many times. At the time of heavy fish mortality in Pasinski's Pond, in February, 1940, a very pronounced stench arose from holes chopped in the ice, the odor being at least in part that of hydrogen sulfide. In the same winter, the stagnant water of Richmond Lake also stank strongly for many days. Continuously throughout the entire period of ice cover (even during the comparatively mild winter of 1940-41), the water from the lower depths of Bog Lake reeked with hydrogen sulfide. The fact that the surface water usually was virtually free from this gas indicates that the gas either was oxidized before it reached the surface, or was held in chemical or physical combination in the lower water.

The possible harm to the fish caused by directly toxic properties of various gases is discussed below. The often more serious effect of these gases is the removal of dissolved oxygen from the water. This oxygen depletion may occur in two ways, by chemical or biochemical oxidation, or by the sweeping action of the gas in bubbling through the water.

Kusnetzow (1935) gave a rather strong argument for the theory that, in some lakes at least, the bacterial oxidation of methane and hydrogen arising from the bottom sediments may be the principal factor in the removal of oxygen from the water in the winter. In lakes in which the oxygen remained at high level throughout the winter he found the amount of methane and hydrogen coming from the bottom to be much less than in the "fish suffocation" lakes, although both types of lakes abounded in water bacteria. He concluded, therefore, that it is not alone the simple respiration of the bacteria, but rather their increased activity in the presence of methane and hydrogen, that exerts heavy demands upon the dissolved oxygen (to the purly chemical oxidation of these gases he attributed an insignificant part).

It is barely possible, of course, that Kusnetzow's explanation may be somewhat in reverse, and that the increased production of methane and other reducing gases may appear as a result, rather than as a cause, of oxygen depletion, since lowered oxygen near the bottom would favor the activities of the anaerobic (gas-producing) bottom bacteria.

The purely mechanical action of gas bubbles in removing oxygen probably is of considerable significance at times (Welch 1935, p. 91; Knauthe 1899). The bubbles of gas may entrap oxygen and carry it to the surface, where it is lost to the atmosphere. The amount of oxygen so removed depends upon the number, size, and character of the gas bubbles, the temperature, and so forth. The last small fraction of the dissolved oxygen is harder to remove than that near or in excess of saturation.

DECAY OF SUSPENDED MATERIAL

Suspended particulate matter in lake water may arise from various sources, chief of which usually is the dead remains of plankton (for the purposes of this discussion living plankton is not termed "suspended"). It may contain also the remains of dead higher plants and animals. Naturally-formed detritus, and occasionally pollutional wastes, may be carried in by streams.

The quantity of material in suspension varies from lake to lake and from time to time, from an amount detectable only upon concentration, to that sufficient to render the water distinctly turbid. In general it is apt to be much greater in rich bodies of water than in those less eutrophic. It is sometimes cyclic, following cycles of plankton abundance.

This material varies in composition, but it is rich in organic matter. It is scarcely heavier than water, and sinks slowly. This probably is particularly true in the winter, not only because the water is slightly denser, but also because it has a greater viscosity at low temperatures (Welch 1935, p. 85). As a consequence of slow settling, the suspended organic material is in contact with the water for a fairly long time.

Since it contains a large proportion of organic substance, it is to be expected that the suspended material is capable of utilizing considerable oxygen. It seems that lake water usually contains large numbers of bacteria, atlhough these numbers may decline somewhat in winter. Henrici (1939) found in Lake Mendota that "under the ice in winter the bacteria are uniformly few in number until the bottom meter is reached, where they show an amazing increase." He pointed out, also, that bacteria in the water are for the most part periphytic, i.e., attached to suspended materials or to living plankton. Blue-green algae especially are collectors of bacteria (Henrici & McCoy 1938). By this means the bacteria are given ready access to the dead plankton material.

The amount of bacterial action depends to a certain extent upon various physical and chemical factors, and upon the kinds of organic matter present. On the whole, the statement of ZoBell (1940) that plank-

ton remains are more readily oxidizable by bacteria than is the dissolved organic matter in the water, probably holds true. However, certain materials, such as chitin, lignin, and humus-like compounds, are less amenable to bacterial attack than the simple carbohydrates and proteins, and may reach the bottom unaltered. The semi-colloidal suspensoids of dystrophic lakes have been said to be relatively resistant to water bacteria.

Bacterial oxidation is of course slower at low temperatures than at higher ones. ZoBell obtained a Q_{10} for water bacteria of about 2.1, in the region 8°-25° C. Short-time (5-day) biochemical oxygen demand tests at 0° give correspondingly lower results than those at 20° (see discussion in the section on B.O.D.). It is of interest to note, however, that the eventual or ultimate B.O.D. may be fully as great at the low temperature as at the higher one.

Many opinions have been expressed regarding the relative importance of suspended material as an oxygen-depleting agent. Birge & Juday (1911, p. xiii), in defining the "zone of decomposition," stated that the dead materials settling into this zone are instrumental in oxygen utilization. Much evidence has been produced by various workers to substantiate this view. Rawson (1939) summarized the theory by saying that "there would seem to be greater possibility that the original explanation was the correct one, i.e., that hypolimnial consumption of oxygen is largely due to decomposition of dead plankton falling through the hypolimnion."

Divergent ideas, however, have been proposed by various writers, such as Drown (1892), Alsterberg (1927), Henrici (1939), and so forth. The theories of some of these workers, in assigning a larger share of the oxygen consumption to various other factors, have greatly minimized the part played by the decay of suspended matter.

Observations of the present investigation indicate rather strongly that, in the lakes studied, the suspended material played probably a large part in the oxygen diminution under the ice. For example, in Pasinski's Pond at times in the winter of 1940-41 the coincident occurrence of a large amount of suspended matter and of a very high oxygen demand (as measured by B.O.D. tests) was too marked to be casual. The argument is strengthened by the correlation observed between B.O.D. and the amount of suspended material at various depths. When the water near the surface was much more turbid with suspended matter than that near the bottom, it also had a much higher B.O.D.

DECAY OF DISSOLVED ORGANIC MATTER

It is difficult to distinguish, entirely, between dissolved and suspended materials, and therefore difficult to judge the relative oxygen-consuming powers. In practical work, distinction usually is made on the basis of passage through a high-speed centrifuge or a fine filter. The "dissolved" material so obtained may include a small proportion of substances which are not true solutes, but very fine suspensoids or colloids.

Birge & Juday (1926) published the results of an extensive study of the organic content of several Wisconsin lakes. They found the amount of dissolved organic matter to be considerably higher in these inland lakes than in the sea, and usually to be several times as great as the amount of organic matter contained in the standing crop of plankton. The dissolved organic matter varied, in the several lakes, from about 6 to about 38 mg. per liter.

This material, according to Birge & Juday, is derived chiefly from plankton, although a small part of it may come from the disintegration of higher plants or from other sources. Its composition is complex, but it is relatively rich in various carbohydrates (only a small part of which, however, is sugars or other simple carbohydrates), and nitrogen in the form of peptides, amino acids, and so forth. Obviously these substances are capable of utilizing rather large quantities of dissolved oxygen (for example, the complete oxidation of only about 12 mg. of carbohydrate per liter would require all of the dissolved oxygen in water saturated at 4° C.). The extent of their oxidation, however, depends upon their suitability and availability as food for the water bacteria. On this question there has been considerable discussion. At least some of the dissolved substances, such as complex nitrogenous compounds, have been held to be very resistant to bacterial action (Krogh 1931, ZoBell 1940). Others, however, such as simple amino acids and carbohydrates, can more readily be utilized by the bacteria, the extent of such use depending upon numbers and kinds of bacteria present and the temperature. In the B.O.D. tests of this study no attempt was made to determine the proportion of the oxygen demand of the water which was due to the dissolved organic matter.

Although not classed as an organic substance, ferrous iron may be mentioned here as being a possible factor in dissolved oxygen reduction. Sometimes present in solution in certain lake waters, particularly of dystrophic lakes, it may, under the proper conditions, be converted into ferric iron, either chemically or biochemically, with the resultant consumption of oxygen. In certain brown-water lakes reported on by Brehm & Ruttner (1926), ferrous iron, of allochthonous origin, was said to exert a very high oxygen demand. In most clear-water lakes, however, probably this factor is a very minor one.

GROUND WATER AND SURFACE INFLOW

In certain lakes subterranean inflow may be of appreciable amount, even in winter. This ground water often is very low or totally deficient in dissolved oxygen, and it may thus reduce the oxygen content of the lake as a whole. Shopinzev (1940) held the large proportion of ground water in the Volga River, in the winter, responsible for the lowered oxygen content of the river. It is questionable, however, that ground water is a significant source of

oxygen reduction in most Michigan lakes in winter, for its flow usually is small.

Inflowing water arising from rain or melting snow or ice on the surface of the lake sometimes is lower in dissolved oxygen than is the water immediately under the ice, and hence upon mixing it may actually lower the oxygen content of the upper layer of water. The total body of water, however, is not affected to any considerable extent, since the inflowing water is comparatively small in volume, and usually carries some dissolved oxygen.

OXYGEN REPLENISHMENT

Once sealed in by a covering of ice, a lake cannot acquire oxygen, as in the summer, by wind agitation. Even the small blessing of surface diffusion is seriously restricted. Advantageously enough, a lake usually enters the winter period with its oxygen concentration at the normal annual maximum, i.e., saturation at 4° C., or about 13 p.p.m. In the deeper, more oligotrophic type of lake this initial oxygen supply may be adequate to carry the lake through the entire winter. But in shallow, organically rich lakes the processes of respiration and decay, discussed above, undoubtedly would consume the oxygen supply long before the end of winter, were that supply not somehow replenished.

Except for artificial aeration, and the ingress of oxygen-bearing water, augmentation of the oxygen supply can be brought about by only one means, photosynthesis. In many lakes, therefore, the maintenance under the ice of a copious oxygen supply is absolutely dependent upon the presence and activity of green plant life.

HIGHER PLANTS

The importance of rooted plants as oxygen producers in winter is not well known. The situation is complicated by great variations in the kinds and numbers of these plants which may be in an active state under the ice cover. Many observations have been made of rooted aquatic plants which were quite green under the ice, particularly in early winter before much snow had fallen. Olson (1932) stated that "higher aquatic plants in many instances die off in the fall. . . . There are a few plants, however, that remain active through the winter, and these can produce oxygen in considerable quantities when light is available." He reported the observation of green aquatic vegetation through the ice in late January, at which time the water in the immediate vicinity of the plants was supersaturated with oxygen. It is not especially uncommon for winter fishermen in spearing shanties on southern Michigan lakes to notice considerable rooted vegetation in a green condition. Early in the winter such plants as Vallisneria and certain pond-weeds may be quite actively vegetative.

However, for most of the higher plants (with particular reference to those inhabiting Michigan winter-kill lakes) winter is usually a time of little activity. With few exceptions, the lakes studied contained very little vegetation in a green condition in the winter. Cattails, bulrushes, and water-lilies were brown at the onset of the ice; coontail, bladderwort, and most pond-weeds died down to a large extent soon after. The large beds of Anacharis which filled Pasinski's Pond were partially green at times, and may have contributed some oxygen to the water. Occasionally in Mud Lake and Green Lake a certain amount of green color was evident in some of the weeds, especially when the ice was bare. On the whole, however, the higher plants probably are a relatively insignificant source of oxygen in these lakes in the winter.

NON-PLANKTON ALGAE

Certain of the filamentous algae occasionally are found in abundance in the winter. It is fairly well established that many algae can thrive at low temperatures, given enough light. Smith (1933, p. 23) defines a group of algae, which he designates "winter annuals," which vegetate in the winter and fruit in early spring. This group includes one or two species of Spirogyra, as well as several single-celled algae. Knauthe (1899) attributed a part of the winter oxygen production in the ponds he studied to filamentous algae.

In Pasinski's Pond, in the winters 1939-40 and 1940-41, a very large mass of Spirogyra was present, especially in the south end of the pond. This material stayed green during a considerable part of each winter; its greeness varied with the amount of snow on the ice. The Spirogyra quite evidently had an appreciable effect upon the dissolved oxygen content of the water (see the section on dissolved oxygen in Pasinski's Pond). In none of the other bodies of water studied were non-plankton algae noted in any appreciable concentrations.

PHYTOPLANKTON

It has long been known that the microscopic plants of the plankton play an extremely important part in the replenishment of dissolved oxygen in lakes, even under the ice. Knauthe (1899) was well cognizant of the interrelations of light, an abundant crop of phytoplankton, and the production of oxygen in ponds in the winter. He found, at times, a very pronounced supersaturation of oxygen, coincident with intense activity of the plankton plants. Griffiths (1936) stated that the oxygen concentration in Long Pool, in February and early March, was "associated with a maximum abundance of phytoplankton, consisting mainly of *Dinobryon, Uroglenopsis,* and *Eudorina.*"

Quantitative information concerning phytoplankton in ice-covered lakes is scarce. Trends of thought of various writers have indicated that (1) the phytoplankton as a whole diminishes in the winter months, (2) diatoms may become relatively abundant in winter at the expense of green and blue-green algae, and (3) there are apt to be large fluctuations from lake to lake and from winter to winter. Whereas some specific studies have been in agreement with these general ideas, other disagree. Kofoid (1903)

found that the Illinois River, as well as an inland lake, contained in the winter a relatively high amount of plankton, of which a fair proportion presumably was phytoplankton. Griffiths reported that, for Long Pool, phytoplankton was "even moderately abundant only during the colder months." In Lake Mendota, in 1916-17 (Birge & Juday 1922), the total phytoplankton was somewhat less in quantity in the winter than in the summer; Microcystis showed relatively little decline; Aphanizomenon reached a peak in early January and fell off sharply in late February; Tabellaria began to increase in late winter. The predominant plant of the nannoplankton in winter was Aphanocapsa, which was little changed from its summer concentration; in late winter Chlorochromonas began to appear in fair abundance.

In their survey of Green Bay, in 1938-39, Williamson et al. (1939) found the net plankton to be very small in amount throughout the entire period of ice cover, and to consist of a few diatoms and very little else. The ice was covered with snow for a large portion of the winter. The bloom of Aphanizomenon which had appeared in November was well dissipated by the time the ice had become solid in January.

In the present investigation no quantitative data regarding plankton were obtained. Nothing like a plankton bloom was observed at any time during the four winters. It is possible that there was considerable phytoplankton present at times, however, for many sudden and large increases of dissolved oxygen were recorded.

BACTERIA

Certain bacteria, such as the green and red sulfur bacteria, possess pigments somewhat related to chlorophyll, and are able to utilize light for photosynthesis. However, according to Van Niel (1935), who has made an extensive study of these photosynthetic bacteria, it is very doubtful that they produce any oxygen. The nature of their action is parallel to, rather than identical with, that of green plants. Carbon dioxide is reduced, but the necessary hydrogen is derived from organic substances or from H_2S, rather than from water.

Although these bacteria cannot properly be considered as direct producers of oxygen, they may have an indirect effect, in that they stabilize substances such as H_2S and CO_2, and thus reduced the potential oxygen demand of the water. It is possible that these bacteria may exist and operate in lakes in the winter, particularly in lakes which contain hydrogen sulfide.

RUN-IN WATER

Inflowing water which arises from rain or melting snow or ice usually contains a few parts per million of dissolved oxygen, and may thus bolster a depleted oxygen content. This effect is often transitory, however, and is usually confined to the upper layers. Nevertheless, such incoming water probably helps occasionally to tide a lake over a perilous period, as perhaps occurred in some of the lakes under observation in 1937-38.

WINTER SUFFOCATION OF FISH

If the oxygen-replenishing agencies fail to produce oxygen as rapidly as it is being consumed, a serious shortage of dissolved oxygen may ensue, and the fish may be endangered. Certain things should be known concerning the suffocation of fish under the ice. How prevalent and how serious is winter-kill? What is the physiological basis for the death of the fish? What are the general consequences of winter-kill? What can be done to prevent it?

INCIDENCE OF WINTER-KILL

The extent of damage by winter suffocation may vary from the loss of only a few fish to the complete or almost complete annihilation of the fish population of a lake. The death of relatively small numbers of fish during any one winter probably indicates only an indirect connection with winter-kill. A certain number of fish succumb, during the winter, to disease, parasites, or accident. Birds are excluded from the water by the ice, and other scavengers are less active in the winter than in the summer; decomposition of fish carcasses proceeds more slowly at low temperatures; and thus quite a few fish which have died during the winter come to the attention of the casual observer at the time of the break-up of the ice.

There are records of the destruction by winter-kill of extremely large numbers of fish. In the mortality in the Racine River, Wisconsin (Hoy 1872) "thousands of barrels" of fish died. According to Olson (1932), 20,000 pounds of dead carp were removed in one day, in the winter of 1928-29, from a small lake in Minnesota. In Crystal Lake, near Gulfport, Illinois, over 80,000 pounds of fish, mostly carp and buffalo, were found dead at the end of the winter of 1939-40 (Illinois Natural History Survey, personal communication). At Georgetown Lake, Montana, in the winter of 1936-37, more than 700,00 trout are said to have perished (King 1937).

In Michigan, especially in such winters as that of the "big freeze-out," 1935-36, many severe fish losses have occurred. In the reports of various observers, references to "many hundreds," "thousands," and "large numbers" appear frequently. Cooper (unpublished report 1936) gave the following estimates of fish killed in certain lakes in southern Michigan, in 1935-36: Bateese Lake, over 200,000; Mud Lake, over 75,000; Green Lake, between 75,000 and 100,000; and Park Lake, over 150,000.

Again in the winter of 1944-45, several lakes in Michigan, as well as in Wisconsin and Minnesota, suffered extremely large winter-kill losses.

Complete destruction of a fish population apparently is very rare. It has been recorded by Knauthe (1899) for a carp pond, but this was an artificial situation. In Pasinski's Pond, in 1939-40, the bluegills were all killed, but most of the bullheads survived. This pond is scarcely typical of southern Michigan lakes, being small and exceedingly rich in organic matter. No other substantiated record of a complete winter-kill of fish in Michigan waters exists.

On the other hand, many lakes which were thought at the time to be entirely killed out have later been found to contain a surviving stock. It is difficult to be certain whether the fish have all been killed in some lakes, because of stream connections through which fish might enter following the kill.

PHYSIOLOGICAL ASPECTS

CAUSE OF DEATH

Mention has been made, in the introduction, of the theories and beliefs of various writers as to the *modus operandi* of winter-kill. Although certain of these writers have blamed such factors as "poisonous" gases (presumably hydrogen sulfide, ammonia, or methane), the weight of majority opinion has placed the responsibility on lowered dissolved oxygen tension. This theory has been fairly well substantiated in the literature.

The present survey presents still more evidence in the same direction. Wholesale death in Pasinski's Pond occurred at the only time during the three winters of investigation there that the dissolved oxygen in the pond fell to 1 p.p.m or less for several consecutive days. Similarly, at other lakes substantial fish mortality has been found to come about at times of extremely low oxygen. This was found to be the case also during the studies made by the Institute for Fisheries Research in the severe winter 1935-36.

However, it must be remembered that almost invariably low dissolved oxygen concentrations under the ice are accompanied by various other adverse conditions. The very processes of decay which consume the oxygen produce, at the same time, carbon dioxide, methane, hydrogen sulfide, and possibly ammonia. Hence any conclusion, *a priori*, that lack of oxygen is indisputably the sole cause of death is unjustified. Complete knowledge must rest on physiological experiments, because the several factors cannot readily be disentangled in nature.

The reasoning is speculative. It is axiomatic that fish die if the oxygen tension remains for any considerable time below a minimum value. But it also is true that the various noxious gases named above, if present in sufficient quantity, can be fatal to fish. Carbon dioxide alone, in high concentration, can kill fish, even in the presence of abundant oxygen. Furthermore, there are complex relationships. To take a common example, the presence of large amounts of carbon dioxide greatly reduces the ability of fish to utilize oxygen at low tensions (Fry 1939, and others). In other words, the toxicity of carbon dioxide increases with lowered oxygen tension.

The literature on winter mortality of fish has insufficient information on which to base any definite conclusions regarding the relative importance of these various factors. Nor do the data of this study give rise to any completely satisfactory deductions. In general, the CO_2 concentrations, although appreciable, were not alarmingly high, and the increase was somewhat gradual (a point apparently of some significance, as discussed below). It is probable that, compared to the dissolved oxygen at its lowest levels, the carbon dioxide was not the most dangerous factor. Also, although the evidence at hand is scant, it appears possible that the amounts of hydrogen sulfide and other poisonous gases which usually were present in the lakes studied were not in excess of the toleration limits of the fish.

Further speculation is fruitless. Suffice it to state that very low dissolved oxygen concentrations are probably the primary cause of death of fish in winter-kill, and that the effects of low oxygen may be augmented by the presence of carbon dioxide, and often of other harmful gases.

TOLERANCES AND ADAPTATIONS

In laboratory determinations of low oxygen tolerance limits of fresh-water fishes, most workers have neglected the lower temperature ranges. Even the experiments at room temperatures, of which there have been many, have produced results in considerable conflict, depending upon experimental method, species of fish, and the effect of various uncontrolled conditions.

Refining and extending a method of field observation used by Smith (1925), Moore (1942) obtained some figures for low-temperature oxygen requirements, that apparently are rather dependable. The experimental fish were held in live boxes in natural waters of various oxygen tensions, and the results are stated in terms of survival or non-survival for a 48-hour period. Control was good, and the effects of handling, pH, and CO_2 probably were minimal. It was found that the "thresholds of many species of fresh-water fishes lie between 1.0 and 2.0 p.p.m. However, some of the less tolerant species may require up to 3.0 p.p.m. or possibly higher." Even at extremely low oxygen concentrations, death did not occur immediately (in some instances not in four hours), indicating that suffocation at low temperatures requires a comparatively long time.

Moore's figures confirm rather well the conclusion of Thompson (1925) that, at low temperatures, "dissolved oxygen concentrations between zero and two parts per million will kill all kinds of fishes." Data of the present investigation are entirely inadequate to establish tolerance limits. However, at certain times, dissolved oxygen concentrations of less than 2 p.p.m. were found, with the apparent survival of the fish. For instance, in Pasinski's Pond in February and March, 1940, some 20 stations were sampled regularly, assuring fairly adequate coverage of the four acres. For the consecutive sampling dates February 26, 28, and March 1, not one dissolved oxygen value of over 1.5 p.p.m. was found at these stations, and most of the values ranged from 0.0 to 1.0 p.p.m. Although the bluegills died, most of the population of the more hardy bullheads lived.

Carbon dioxide tolerances of fishes have been studied by many writers, such as Wells (1918), Powers and associates (Powers 1938, and other papers), and Black and his associates (Irving, Black, & Safford 1941; Fry 1939; etc.). Powers has concluded

that fish can satisfactorily absorb oxygen in the presence of carbon dioxide in the concentrations usually found in nature. The factor which in his opinion often causes mortality is a sudden increase in CO_2, to which the fish cannot adjust themselves. No special reference is made to the conditions of winter, when abnormally high carbon dioxide tensions may occur.

It has been claimed that fish exhibit avoiding reactions toward low dissolved oxygen (Thompson 1925) and toward high carbon dioxide (Wells 1918). However, it was observed many times in this study that when an open hole is maintained in the ice, at times of low oxygen in the water, the fish will crowd into the open hole, and will remain there until they succumb, even though the oxygen drops to zero while nearby water still contains oxygen. For example, in Richmond Lake on February 18, 1940, the surface water in an open hole contained only 0.4 p.p.m. of dissolved oxygen, while that at a station not far away had 1.9 p.p.m. Yet the hole was full of dead and dying fish. Similarly, in Pasinski's Pond, on February 19, 1940, there were hundreds of dying fish in the open hole, and at the same time the oxygen at a station only 40 feet away was 2.8 p.p.m. It is possible that the avoidance reactions of the fish are relatively slight at such low temperatures. Also, it seems likely that the tendency for the fish to move into an open hole and stay there is conditioned by a positive reaction toward light or toward open water, or by the opportunity to gulp air at the surface.

It is known that there are considerable differences in the sensitivity of various species of fish to adverse conditions. Various listings of the order of resistance have been given. Fry (1939) listed them on the basis of the effect of carbon dioxide on oxygen utilization. Moore (1942) gave the order in which several species resisted diminished oxygen tension at low temperature. Almost all authors agree that in general such species as sunfish, yellow perch, and black bass are more sensitive to lowered oxygen tension and other adverse conditions than those species commonly called rough fish, such as bullheads, carp, and dogfish. It is probable that within species there are relatively tolerant and relatively susceptible physiological races, and that hereditary individual differences exist within single populations.

Differences in sensitivity also exist because of differences in age, physiological condition, and (possibly) sex. Moore concluded that older fish can withstand winter oxygen depletion better than can younger ones, since the metabolic rate decreases with increasing age. Fish in poor physiological condition, or those weakened by injury, parasites, or disease no doubt become victims of winter-kill more readily than the more hardy individuals.

Certain fish species have been shown to have special physiological adaptations which enable them to survive conditions that otherwise might be catastrophical. An example is the mud minnow (Umbra). This fish is the only species known to be present in Bog Lake, where it has maintained itself through countless winters (the stock could not have been replaced by immigration in recent decades, for the lake has no water connections). During many of these winters, the lake must have been completely devoid of oxygen for considerable periods, yet the mud minnows survived. The explanation probably lies in the ability of this fish to utilize atmospheric oxygen. It has been demonstrated (Geyer & Mann 1939, and others) that Umbra can exist in water of low oxygen concentration if it is allowed access to the surface, in order to gulp air. It is not very clear just how the fish can obtain air in the presence of an ice cover, but it is possible that cracks in the ice, and air pockets under the ice, allow enough contact with the atmosphere to fulfill the relatively small needs of the fish in cold water. Perhaps there is a possibility that the mud minnow may undergo actual hibernation, perhaps buried in the muck of the bottom, for part or all of the winter, although Morgan (1939, p. 321) has raised the question of the existence of true winter dormancy in fishes. At any rate, a very sluggish fish would consume very little oxygen.

CONSEQUENCES

Heavy winter-kill in a lake may reduce the fish population to such an extent that fishing for the next season or two is very unproductive. Unfortunately, no really quantitative records are available for Michigan lakes regarding the fishing success in the first and second summers following a heavy winter mortality. In fact, the knowledge that a lake has suffered a large loss often keeps most fishermen away from that lake for a year or two, and hence a creel census would be of small value.

Within a certain range, the effect upon the fishing is more or less in proportion to the extent of the kill of the game fish. However, in some lakes, and with a not too heavy loss, a different and perhaps even desirable result may obtain. It is known that many Michigan lakes are over-populated with various game fish to the extent that extreme stunting occurs. It is altogether probable that a considerable reduction in numbers of these fish results in faster growth of the remainder, and hence in fewer, but larger, fish becoming available to the angler (Beckman 1941, 1943).

It appears likely that, following a winter-kill, the fish population recovers to a large degree within a very few years, and eventually becomes restabilized at its original level. Rebuilding of the population may be effected by artificial stocking, by immigration through connecting streams, or by the fecundity of a surviving parent stock. An apparently well substantiated instance of a recovery from a surviving stock is that of Goose Lake, in Jackson County. This lake was considered good fishing for largemouth bass. It was hit severely by winter-kill in 1935-36, when it was popularly supposed to have been almost entirely depopulated of fish. Natural reinvasion could not take place because the lake has neither inlet nor outlet, and there were no recorded artificial plantings

of bass between 1936 and 1941. Fishing conditions in the lake after the spring of 1936 have been described by Haines (1941). Although admittedly based on a small amount of observation, his information is of interest. In 1938, two years after the winter-kill, he found that fishing was still rather poor, and that the bass taken were small. But in 1941, after a total of five years, he made several good catches of large bass.

Species differences in tolerance of fishes to unfavorable conditions often brings about a differential winter-kill. In general the game fish are more sensitive than are the rough fish, and several reports in the literature have indicated that the game fish suffer more damage than the non-game species. As already mentioned, the winter-kill of 1939-40 killed all the bluegills in Pasinski's Pond, but destroyed relatively few bullheads. An apparent exception to this general rule was found by Aitken (1938), who reported, "Although many fish died the winter of 1936 they were mostly carp, buffalo, and sheepshead whose loss was probably beneficial to the lakes."

Reports made by fishermen and other interested persons probably are influenced by the propensity of the observer toward noticing game fish, his tendency to neglect to observe minnows and other small fish, and at times his inability to recognize other than the game species. Nevertheless, the figures available, as regards winter-kill in Michigan lakes, distinctly show the game species to be the ones most affected. As Smith (1941) and others have pointed out, this discrimination has the effect of leaving a population, and a brood stock, composed of a large proportion of rough fish. In this manner the species balance between predator fish, game and food fish, and forage fish may be seriously disrupted. It may well be, however, that this balance becomes restored, through the workings of ecological forces, within a relatively few years.

Various other animals besides fish sometimes are victims of winter-kill. Kochs (1891) reported the death of very large numbers of frogs. Olson (1932) also stated that frogs are subject to winter suffocation. In the present investigation, dead tadpoles were observed a few times, but never any dead adult frogs, nor are frogs specifically mentioned in the reports of winter-kill in Michigan lakes.

Many dead snails were observed after the breakup of the ice, particularly in Green Lake, but it is not known whether they were killed by low oxygen or died from other causes. Similarly, although a few dead mussels, crayfish, and turtles may be seen along the shore of a lake after the ice melts, it is questionable that they are the victims of winter-kill, since their death in large numbers has seldom been reported.

The plankton invertebrates probably are destroyed in large numbers in some waters. Kofoid (1903) recorded the "practical extinction of the plankton" in places in the Illinois River during a winter of heavy fish mortality. However, since many of the plankton animals normally are subject to vast changes in numbers, cyclic or otherwise, and are equipped to weather adverse conditions by means of winter eggs or other resistant forms, it is likely that winter-kill is by no means a complete catastrophe to them. Benthic invertebrates, such as aquatic insect larvae and nymphs, no doubt are affected to some extent.

PREVENTIVE AND REMEDIAL MEASURES

Lake conditions conducive to winter-kill are more fitly subject to prevention than to cure. Once a lake develops an oxygen deficiency to the point where fish are in distress, it is doubtful if artificial means can avert considerable destruction. On the other hand, there are certain measures which, if applied early enough in the winter, may go far toward preventing harmful conditions from arising. In the following discussion not only are these methods considered, along with the extent of their economic feasibility, but also brief attention is given to sundry procedures, proposed or even actually attempted by various workers, which are neither theoretically nor practically sound.

FLOWING WATER

If an appreciable flow of water through a lake can be maintained throughout the winter, and if the inflowing water always carries a reasonably large amount of dissolved oxygen, it is logical to suppose that the water of the lake, at least within the path of flow, can be kept supplied with oxygen. Mud Lake furnishes an example of a stream's having considerable influence upon the oxygen content of the lake water. Hubbs & Eschmeyer (1938) discussed the possibility of diverting a natural stream into a lake in order to prevent winter-kill. However, it will generally be impractical to bring about such a diversion. Furthermore, there is not always assurance that the stream will remain aerated, since it in turn may arise in another lake where low oxygen also prevails.

Water from wells perhaps may be utilized as a source of supply for some ponds, but as a rule ground water contains little oxygen and therefore must be artificially aerated before it enters the pond. The results of an experimental use of such a water supply at Pasinski's Pond, discussed above, showed little if any improvement in conditions which could be attributed to the well water, presumably because the supply of oxygen it brought in was insufficient to overcome the large oxygen demand which existed in the pond.

RAISED WATER LEVELS

Smith (1941), Hubbs & Eschmeyer, and others have recommended raising the lake level as a means of preventing winter-kill by enlarging the initial supply of oxygen. Probably it is feasible to raise the water level of some shallow lakes by a foot or two in the fall or early winter; whether this additional amount of water can furnish enough oxygen to meet the demands of decaying organic material is doubtful. As discussed above, it seems likely that the average shallow lake of the winter-kill type uses, during a

long winter, more than the amount of oxygen with which it starts the winter, the balance being made up by photosynthetic production under the ice.

HOLES IN THE ICE

For no one knows how many decades, fishermen, conservationists, and others have attempted to relieve winter suffocation by cutting holes in the ice. Even scientific writers have recommended the procedure (Wickliff n.d., and others). Presumably these workers subconsciously postulate some such analogy as lifting the trap-door to a dungeon, thus to allow its occupants access to air and to life. Or there may be present the notion, expressed in a newspaper account (Milwaukee Sentinel 1939), that holes in the ice will "allow the poisonous gases which mean death to the fish to escape." At any rate, despite many published statements in deprecation (Knauthe 1899, Hubbs & Eschmeyer 1938, Milwaukee Journal 1939, Smith 1941, and others), the practice still has many ardent followers.

The seal of an ice cover is not nearly so perfect as is often supposed. Cracks, pinholes, and air-pockets would relieve any very great pressure that a dissolved gas might build up, and allow the escape of the gas. The very fact that almost invariably the greatest concentrations of methane, hydrogen sulfide, and carbon dioxide are near the bottom rather than near the surface would indicate that it is not the mere presence of ice that prevents their escape from the water.

In the absence of agitation, diffusion of air through the surface film of water is exceedingly slow and small in amount. Any appreciable aeration of the water of a lake by mere contact with the air over the area of a number of holes in the ice is impossible. It is true that if agitation can be accomplished, as by wind, much air can be put into the water. But, as those who have tried it know, the task of removing the ice from any appreciable area of the water is a large one indeed (to clear one acre of ice one foot thick would require the removal of 1,100 tons of ice). Artificial agitation, by outboard motors or other propeller devices, unless used in impractical numbers, cannot affect a large enough proportion of the lake's volume to be of any significant aid.

A popular theory is that fish are benefited by coming to the surface at open holes and gulping air. However, most fish are fitted primarily to extract their oxygen from that dissolved in the water, and are poorly equipped to utilize atmospheric oxygen. It is held by Powers (Powers, Shields, & Hickman 1939, and other papers) that gulping may actually be detrimental, because it brings about rapid changes in carbon dioxide tension.

Holes cut in the ice may result in actual harm because of their attraction for fish. As described above, fish tend to congregate at an open hole, and may remain there until conditions in that immediate place become fatal to them, even though there is better water not far away.

ARTIFICIAL AERATION

Various experiments, in Michigan and elsewhere, in the artificial aeration of ice-bound lakes by means of water or air pumps have been described above, in the section on Experimental Studies. Almost all of these experimenters have reached the conclusion that pumping methods are wholly inadequate to aerate even a fair-sized body of water.

The difficulty with almost any pumping method is in getting aeration for any appreciable distance from the seat of operations. Furthermore, the effects of the pumping usually are quite transitory.

Perhaps the possibilities of pumping have not entirely been exhausted, and further experimentation may be justified. It is possible that efficient air or water pumping over a long period of time could introduce considerable oxygen into a very small body of water, such as a farm pond. Certain precautions should be used, for instance to avoid stirring up bottom materials and thus making them more readily available for bacterial oxidation (Hubbs & Eschmeyer 1938). Pumping would have more chance of being effective if started prior to the attainment of extremely bad conditions, rather than after the oxygen is well exhausted. After the water has developed a large oxygen demand, the small amounts of oxygen that are added are quickly consumed. There seems to be little hope that pumping methods will ever be found to be feasible for larger bodies of water.

CHANGES IN VEGETATION

Since aquatic vegetation is known to be a producer of oxygen, under the proper conditions, it has been proposed (Aitken 1938) that winter aeration of lakes could be accomplished by increasing the amount of vegetation present. As has been pointed out above, the higher plants usually are responsible for relatively little oxygen production during the winter. During periods of snow cover, there is little photosynthesis, and the dead remains of plants may become an agent of oxygen consumption. It is therefore doubtful that any aid in alleviating winter suffocation is to be derived from the artificial propagation of plants.

Plankton plants can be increased by the addition of fertilizer to the water, but excess fertilizer, and the remains of plankton algae that die, have a large demand for oxygen. The balance, therefore, is so delicate that tampering is not justified in the light of the present knowledge concerning artificial fertilization of lakes.

In extremely weedy lakes, it is perhaps more desirable from the standpoint of winter-kill prevention to decrease, rather than increase, the amount of rooted vegetation, since the winter decay of water weeds may use part of the oxygen supply. However, the removal of rooted vegetation from a lake presents many difficulties, and probably should not be considered as an economically sound method.

SNOW REMOVAL

It has been pointed out (in the section on Light Penetration) that there is a definite relationship between the amount of light penetrating the snow and ice cover and the dissolved oxygen content of the water. The presence or absence of a long-continued snow cover on a lake can mean the difference between safety and doom for the fish. It is therefore apparent, and has been mentioned by several authors (Hubbs & Eschmeyer 1938, Smith 1941, and others), that by far the best single method of preventing winter-kill, from a theoretical viewpoint, is the removal of snow from the ice. Moreover, such removal should not wait until dangerous conditions develop, but should be carried out regularly after each major snowfall.

Practically, the method offers many difficulties. Large-scale snow scraping entails the use of power machinery, which is rather costly, and which requires fairly heavy ice for safe operation. Hand shovelling is extremely slow and laborious. There may be merit in such schemes as that of using road-scraping machinery at times when it otherwise would be idle, or that of making a community project out of clearing the ice of snow for the additional purpose of providing skating. Furthermore, the effort could be somewhat lessened by clearing only strips, with alternating windrows of piled-up snow (which might, however, be scattered back onto the cleared areas by subsequent winds). On the whole it is likely that, although the method may be feasible for relatively small bodies of water, it could not be applied to all of the large winter-kill lakes of southern Michigan.

As discussed above, there is considerable promise in the method of removing snow by means of a stream of water, pumped from under the ice. The snow need not be thoroughly melted; it has only to be wet down into a slush. Upon refreezing, it forms a layer of rough ice, which although rather cloudy nevertheless is much less opaque to the light's rays than is snow. The feasibility of applying this method to any considerable area has not yet been determined, but the possibilities seem to warrant further experimental application.

FISH REMOVAL

The removal of fish from a lake subject to winter-kill may be directed toward accomplishing one of two objects. The effect sought may be the diminution of the oxygen demands of the fish by removing a part of them, as in the experiment described by Olson (1932), in which 160,000 pounds of carp were removed from a small lake in the (vain) hope of saving the game fish. As discussed above, the oxygen consumption by fish probably is a very small part of the total oxygen utilization in the water under the ice, and hence the removal of part of the fish will have comparatively little effect in maintaining the oxygen supply.

Smith (1941) discussed the removal of fish (presumably game fish) for another purpose, that of taking them from the danger of winter-kill, and transferring them to deeper lakes where they will be safe. This procedure is a logical one, and in many instances when the threat of disaster is imminent, it may be an advisable thing to do. However, rescue operations in the winter are difficult and costly, and should be considered only as an emergency measure.

SUMMARY AND CONCLUSIONS

In the past, comparatively few studies have been made of winter conditions in lakes, largely because of the difficulties of winter field work. There are, however, many limnological aspects of lakes in winter which are worthy of observation. A cover of ice and snow brings about striking changes in the water. By interfering not only with gaseous exchange, but also with photosynthesis, this cover may have a great effect on the dissolved gases of the water, particularly on the oxygen balance. Among the disasters which may occur when this balance is adversely upset, the most dramatic and economically most important is the destruction of fish by suffocation.

Winter-kill of fish has been recorded many times in the last half-century, in Europe as well as in North America. In this country it is of more or less common occurrence in several north central states. In Michigan, it has occurred in many lakes (though in a relatively small proportion of all of the lakes of the state). There have been kills in many winters, the most notable of which, in recent years, were those of 1935-36 and 1944-45, during which untold hundreds of thousands of fish perished.

The dissolved oxygen content of the water under the ice furnishes a usable and reliable index to chemical conditions related to the well being of the fish. The oxygen concentration varies, sometimes abruptly, throughout the winter and from one winter to another. The greatest and most sudden fluctuations occur in shallow, extremely eutrophic lakes. The dissolved oxygen in a deeper, less eutrophic lake was found to remain remarkably constant throughout the period of ice cover. In respect to dissolved oxygen, a small pot-hole bog lake showed even greater extremes than shallow hard-water lakes.

Of the four winters of the investigation, in only that of 1939-40 did serious conditions develop in the lakes under observation. During that winter the ice was covered with snow for a comparatively long time. In the winters of 1937-38 and 1940-41 snow coverage was of short and irregular duration. In 1942-43 a heavy snow blanket was present for three or four weeks early in the winter, but was dissipated in time to avert the development of dangerous conditions.

Changes in oxygen concentrations, even from week to week, were definitely correlated with changes in the depth of snow on the ice. Measurements of light intensities showed that only a very small amount of light penetrates through even a few inches of snow. Unquestionably a foot or more of dry snow transmits too little light to actuate photosynthesis. On the other hand, ice, even though it is cloudy, permits the penetration of considerable light.

It is probable that the respiration of fish, other animals, and plants plays an insignificant part in the depletion of the oxygen. The main oxygen consumption comes about through the bacterial decay of organic matter, which is largely derived from dead plankton, and is either suspended or dissolved in the water or lies in the form of a mucky deposit on the lake bottom. This bottom deposit also may act indirectly to utilize oxygen, through the anaerobic production of methane and other reducing gases, which in turn are oxidized in the water. The relative importance of each of these organic materials in oxygen utilization is not known, but the correlation of oxygen depletion with general organic richness of the lake is clear-cut. Oxygen consumption is a continuous process throughout the winter, but may be subject to some degree of influence by changes in conditions of temperature and light.

Opposed to oxygen depletion is its production by photosynthesis. In this production, in winter, higher plants are involved to only a minor extent; the chief oxygen output is that of the phytoplankton. The amount of photosynthesis varies greatly, in accordance with the amount of light which penetrates the ice and snow cover.

Winter-kill of fish is principally a matter of suffocation caused by a lack of sufficient dissolved oxygen. High concentrations of carbon dioxide or other harmful gases are contributing factors. The oxygen requirements of fish are comparatively low at low temperatures; but nevertheless certain minimal oxygen thresholds exist beneath which fish cannot indefinitely survive. Different species show differences in tolerance, and hence differential kills occur.

The mortality varies from that of a few fish to the destruction of almost the entire population. Total kill is rare; and, when a residue fish stock is spared, recovery by natural propagation probably is largely completed within a few years, provided a second kill does not occur meanwhile. The detrimental effect upon fishing may be great for the first year or so, however, and the reputation of the lake for fishing is likely to suffer. The effects of winter-kill may not always be altogether deleterious, however, for the thinning of a large and stunted population may result in increased growth of the surviving fish. A heavy winter-kill may tend to disrupt the species balance, by differentially killing the more sensitive species.

Once a lake has developed intense winter stagnation, usually little relief can be secured from the application of artificial measures. Cutting holes in the ice does virtually no good, because air cannot enter the water, by diffusion alone, in any appreciable quantity. These holes may even be harmful, because fish tend to congregate in an open hole and hence to deplete the oxygen in that immediate locality. Nearly all pumping procedures have been found not to be feasible, especially if large bodies of water are involved.

Both theoretical considerations and the results of experimentation indicate snow removal to be a logical and perhaps feasible method for the prevention of winter-kill. The economic practicability of the method is still largely unknown. For small lakes, particularly those which are important fishing waters, it holds considerable promise.

REFERENCES CITED

Aitken, W. W. 1938. The story of Iowa's fish. Bull. 2, Iowa State Conserv. Feder. 1-23.

Allgeier, R. J., W. H. Peterson, Chancey Juday, & E. A. Birge. 1932. The anaerobic fermentation of lake deposits. Int. Rev. der ges. Hydrobiol. und Hydrog. **26:** 444-461.

Alsterberg, Gustaf. 1927. Die Sauerstoffschichtung der Seen. Botan. Not. (1927): 255-274.

American Public Health Association. 1936. Standard methods for the examination of water and sewage. 8th ed. New York, N. Y. xiv + 309.

Atkins, W. R. G., G. L. Clarke, H. Pettersson, H. H. Poole, C. L. Utterback, & A. Ångström. 1938. Measurement of submarine daylight. Journal du Conseil Intern. L'Explor. Mer **13:** 1-21.

Beckman, W. C. 1941. Increased growth rate of rock bass, Ambloplites rupestris (Rafinesque), following reduction in the density of population. Trans. Am. Fish. Soc. **70:** 143-148.

1943. Further studies on the increased growth rate of the rock bass Ambloplites rupestris (Rafinesque), following the reduction in density of the population. Trans. Am. Fish. Soc. **72:** 72-78.

Birge, E. A., & Chancey Juday. 1911. The inland lakes of Wisconsin. The dissolved gases of the water and their biological significance. Wisc. Geol. and Nat. Hist. Surv. Bull. **22:** xx + 259.

1922. The inland lakes of Wisconsin. The plankton. I. Its quantity and chemical composition. Wisc. Geol. and Nat. Hist. Surv. Bull. **64:** 1-222.

1926. Organic content of lake water. Bull. U. S. Bur. Fish. **42:** 185-205.

1929. Transmission of solar radiation by the waters of inland lakes. Trans. Wisc. Acad. Sci., Arts, Lett. **24:** 509-580.

Black, C. S. 1929. Chemical analyses of lake deposits. Trans. Wisc. Acad. Sci., Arts, Lett. **24:** 127-133.

Brehm, V., & F. Ruttner. 1926. Die Biocönosen der Lunzen Gewässer. Int. Rev. der ges. Hydrobiol. und Hydrog. **16:** 281-391.

Brode, J. S. 1938. The denizens of Crater Lake. Northwest Science, Cheney, Wash. **12:** 50-57.

Burr, George O., & M. M. Burr. 1934. A rapid survey instrument for the measurement of light intensity under water. Ecology **15:** 326-328.

Chandler, D. C. 1942. Limnological studies of western Lake Erie. II. Light penetration and its relation to turbidity. Ecology **23:** 41-52.

Clarke, G. L. 1939. The utilization of solar energy by aquatic organisms. Prob. Lake Biology, A.A.A.S. Publ. **10:** 27-38.

Cooper, G. P. 1936. The effects of the 1935-1936 winter-kill of fishes in the following lakes: Batteese, Mud, Stoffer's, Sugarloaf, and Park. Inst. Fish. Res. Report No. 351 (unpubl.).

Croxton, W. C., W. B. Thurman, & T. Shiffer. 1937. The penetration of light through snow and ice cover. Minn. Acad. Sci. **5:** 50-53.

Dorsey, N. E. 1940. Properties of ordinary water-substance. Reinhold Publ. Corp., New York, N. Y. xxiv + 673.

Drown, Thomas H. 1892. On the amount of dissolved oxygen in the water of ponds and reservoirs at different depths in winter, under the ice. Mass. St. Bd. Health, Annual Report **24:** 333-342.

Ellis, M. M. 1934. A photoelectric apparatus for turbidity and light penetration measurement. Science **80:** 37.

Evermann, B. W., & H. W. Clark. 1920. Lake Maxinkuckee. A physical and biological survey. Indiana Dept. Conserv. Publ. No. 7. **1:** 1-660.

Fry, F. E. J. 1939. The position of fish and other higher animals in the economy of lakes. Prob. Lake Biology, A.A.A.S. Publ. **10:** 132-142.

Gardner, J. A., & George King. 1923. Respiratory exchange in fresh-water fish. Part VI. On pike (Esox lucius). Biochem. Jour. **17:** 170-173.

Gardner, J. A., & C. Leetham. 1914. On the respiratory exchange in fresh-water fish. Part I. On brown trout. Biochem. Jour. **8:** 374-390.

Geyer, Fritz, & Hans Mann. 1939. Die Atmung des Ungarischen Hundfisches (Umbra lacustris Grossinger). Zool. Anzeiger 15.

Griffiths, B. M. 1936. The limnology of the Long Pool, Butterby Marsh, Durham: an account of the temperature, oxygen-content, and composition of the water, and of the periodicity and distribution of the phyto- and zooplankton. Jour. Linn. Soc.-Bot. **50:** 393-416.

Haines, D. H. 1941. Lake and stream column, Ann Arbor News, Ann Arbor, Mich. July 19, 1941.

Hand, I. F., & R. E. Lundquist. 1942. Preliminary study of radiation penetration through snow. Central Snow Conference, Proceedings, Mich. State Coll. (lithographed) **1:** 42-44.

Henrici, A. T. 1939. The distribution of bacteria in lakes. Prob. Lake Biology, A.A.A.S. Publ. **10:** 39-64.

Henrici, A. T., & Elizabeth McCoy. 1938. The distribution of heterotrophic bacteria in the bottom deposits of some lakes. Trans. Wisc. Acad. Sci., Arts, Lett. **31:** 323-361.

Higgins, Elmer. 1932. Progress in biological inquiries, 1931. App. III to Report U. S. Comm. Fish. for 1932: 451-529.
1933. Progress in biological inquiries, 1932. U. S. Bur. Fish. 1933: 1-383.

Hoy, P. H. 1872. Mortality of fish in Racine River. Proc. A.A.A.S. 21st meeting: 198-199.

Hubbs, Carl L., & R. W. Eschmeyer. 1938. The improvement of lakes for fishing. Bull. Inst. Fish. Res., Mich. Dept. Conserv. 1-233.

Irving, Laurence, E. C. Black, & Virginia Safford. 1941. The influence of temperature upon the combination of oxygen with the blood of trout. Biol. Bulletin **80:** 1-17.

Jääskeläinen, Viljo. 1930. Fiskarna och fisket i Yskjärvi på Karelska näset. Med hänsyn särskilt till massdöden bland fiskarna i sjön. (Fishes and fishing in Lake Yskjärvi, with special reference to wholesale mortality of fishes in the lake.) Finlands Fiskerier (Lantbruksstyr Meddel. 208) **11:** 55-71.

Jenkin, P. M. 1937. Oxygen production by the diatom Coscinodiscus excentricus Ehr in relation to submarine illumination in the English Channel. Jour. Marine Biol. Assoc. **22:** 301-343.

Jewell, Minna E., & H. W. Brown. 1929. Studies on northern Michigan bog lakes. Ecology **10:** 427-475.

Juday, Chancey, E. A. Birge, & V. W. Meloche. 1941. Chemical analyses of the bottom deposits of Wisconsin lakes. II. Second report. Trans. Wisc. Acad. Sci., Arts, Lett. **33:** 99-114.

Kalitin, N. N. 1930. The measurements of the albedo of a snow cover. Monthly Weather Rev. **58:** 59-61.
1931. Die Strahlungseigenschaften der Schneedecke. Gerl. Beitr. Geophys. **34:** 354-366.

King, Bernard. 1937. Private communication to Michigan Conservation Dept., June 19, 1937.

Knauthe, Karl. 1899. Beobachtungen über den Gasgehalt der Gewässer im Winter. Biol. Centralb. **19:** 783-799.

Kochs, W. 1891. Ueber die Ursachen der Schädigung der Fischbestände im strengen Winter. Biol. Centralb. **11:** 498-508.

Kofoid, C. A. 1903. The plankton of the Illinois River, 1894-1899, with introductory notes upon the hydrography of the Illinois River and its basin. Part I. Quantitative investigations and general results. Bull. Illinois State Lab. Nat. Hist. **6:** 95-629.

Krogh, A. 1931. Dissolved substances as food of aquatic organisms. Biol. Reviews and Biol. Proc. Cambr. Phil. Soc. **6:** 412-442.

Kusnetzow, S. I. 1935. Microbiological researches in the study of the oxygenous regimen of lakes. Verhand. der Intern. Ver. Limn. **7:** 562-582.

Linstedt, Ph. 1914. Respiration and metabolism of cold-blooded animals. Zeit. Fisch. **14:** 193-245.

Lühder, Wilhelm. 1871. Ersticken der Fische in strengen Wintern. Mitth. Naturwiss. Ver. Neu-Vorpommern, Rügen **3:** 86.

Milwaukee Journal. 1939. Fish life now enters its most critical time. Milwaukee Journal, January 1, 1939.

Milwaukee Sentinel. 1939. Fish poisoned in White Lake. Milwaukee Sentinel, February 15, 1939.

Miyadi, Denzaburo. 1934. Oxygen absorption of the lake deposit. Proc. Imp. Acad. Tokyo **10:** 236-239.

Moore, W. G. 1942. Field studies on the oxygen requirements of certain fresh-water fishes. Ecology **23:** 319-329.

Morgan, A. H. 1939. Field book of animals in winter. G. P. Putnam's Sons, New York, N. Y. xv + 527.

Mortimer, C. H. 1941-1942. The exchange of dissolved substances between mud and water in lakes. Jour. Ecology **29:** 280-329; **30:** 147-201.

Naber, Helmut. 1933. Die Schictung des Zooplanktons in holsteinischen Seen und der Einfluss des Zooplanktons auf den Sauerstoffgehalt der bewohnten Schichten. Arch. Hydrob. **25:** 81-132.

Olson, T. A. 1932. Some observations on the interrelationships of sunlight, aquatic plant life and fishes. Trans. Am. Fish. Soc. **62:** 278-289.

Pearsall, W. H., & Philip Ullyott. 1933. Light penetration into fresh water. I. A thermoionic potentiometer for measuring light intensity with photo-electric cells. Jour. Exper. Biol. **10:** 293-305.
1934. Light penetration into fresh water. III. Seasonal variations in the light conditions in Windermere in relation to vegetation. Jour. Exper. Biol. **11:** 89-93.

Powers, E. B. 1938. Factors involved in the sudden mortality of fishes. Trans. Am. Fish. Soc. **67:** 271-281.

Powers, E. B., A. R. Shields, & Mary E. Hickman. 1939. The mortality of fishes in Norris Lake. Jour. Tenn. Acad. Sci. **14:** 239-260.

Rawson, D. S. 1939. Some physical and chemical factors in the metabolism of lakes. Prob. Lake Biology, A.A.A.S. Publ. **10:** 9-26.

Regnard, Paul. 1891. Recherches expérimentales sur les conditions physiques de la vie dans les eaux. Libraire de L'Académie de Médecine, Paris. vii + 500.

Sauberer, Franz. 1938. Versuche über spektrale Messungen der Strahlungseigenschaften von Schnee und Eis mit Photoelementen. Meteor. Zeitschrift **55:** 250-255.

Sheppard, L. C. 1938. Saving fish in frozen lakes. Outdoor Life **81:** 12.

Shopinzev, B. A. 1940. Hydro-chemical regime of the ice-covered Volga River in connexion with the death of fish observed during winter 1939. Comp. Rend. Acad. Sci. Moscou **26:** 670-673.

Smith, Frank. 1925. Variations in the maximum depth at which fish can live during summer in a moderately deep lake with a thermocline. Bull. U. S. Bur. Fish. **41:** 1-7.

Smith, G. M. 1933. The fresh-water algae of the United States. McGraw-Hill Book Company, New York, N. Y. xi + 716.

Smith, Lloyd L. 1941. Facts on winter fish mortality. The Conservation Volunteer, Minn. Dept. Conserv. **1:** 32-36.

Snieszko, S. F. 1941. Pond fish farming in Poland. A Symposium of Hydrobiology, Univ. Wisc. Press: 227-240.

Sweetman, H. L., & H. E. Warfel. 1936. Fish mortality produced by oxygen deficiency. Science **84:** 314-315.

Thams, Chr. 1938. Über die Strahlungseigenschaften der Schneedecke. Gerl. Beitr. Geophys. **53:** 371-388.

Theriault, E. J. 1927. The oxygen demands of polluted waters. Public Health Bull. No. 173, U. S. Publ. Health Serv. x + 185.

Thompson, D. H. 1925. Some observations on the oxygen requirements of fishes in the Illinois River. Illinois Nat. Hist. Surv. Bull. **15:** 423-437.

Titus, Harold. 1936. The Old Warden on smothered fish. Field and Stream, July, 1936: 30-31.

Umbreit, W. W., & Elizabeth McCoy. 1941. The occurrence of actinomycetes of the genus Micromonospora in inland lakes. A Symposium of Hydrobiology, Univ. Wisc. Press: 106-114.

Utterback, C. L. 1933. Variations in visible solar light during submarine measurements. Science **77:** 118-119. 1941. The penetration and scattering of solar and sky radiation in natural water bodies of the Pacific Northwest. A Symposium of Hydrobiology, Univ. Wisc. Press: 45-59.

Utterback, C. L., L. D. Phifer, & R. J. Robinson. 1942. Some chemical, planktonic and optical characteristics of Crater Lake. Ecology **23:** 97-103.

Utterback, C. L., & R. E. Wilson. 1940. Submarine illumination in photometric units. Jour. Optical Soc. Amer. **30:** 136-139.

Van Niel, C. B. 1935. Photosynthesis of bacteria. Cold Spring Harbor Symposia on Quantitative Biology **3:** 138-150.

Waksman, S. A. 1941. Aquatic bacteria in relation to the cycle of organic matter in lakes. A Symposium of Hydrobiology, Univ. Wisc. Press: 86-105.

Welch, P. S. 1935. Limnology. McGraw-Hill Book Company, New York, N. Y. xiv + 471.

Wells, M. M. 1918. The reactions and resistance of fishes to carbon dioxide and carbon monoxide. Illinois State Lab. Nat. Hist. Bull. **11:** 557-571.

Whitney, L. V. 1938. Microstratification of inland lakes. Trans. Wisc. Acad. Sci., Arts, Lett. **31:** 155-173.

Wickliff, E. L. n.d. Ice and its importance to fish life. Ohio Div. of Conserv. Bull. **28:** 1.

Williamson, B. L., John Greenbank, & E. P. Miller. 1939. Investigation of the pollution of the Fox and East Rivers and of Green Bay in the vicinity of the City of Green Bay. Wisc. St. Bd. Health and the Green Bay Metro. Sewerage Comm. (mimeographed) 1-242.

Wilson, L. R. 1935. Lake development and plant succession in Vilas County, Wisconsin. Part I. The medium hard water lakes. Ecol. Monog. **5:** 207-247.

Zinn, D. J., & J. D. Ifft. 1941. A new limnophotometer with a special adaptation for the measurement of the penetration of light through ice under natural conditions. Ecology **22:** 209-211.

ZoBell, C. E. 1940. Some factors which influence oxygen consumption by bacteria in lake water. Biol. Bulletin **78:** 388-402.